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THE RESPONSES OF SUGAR-CANE TO FERTILIZERS

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Summary

Average standardized responses of plant-canes and ratoons to nitrogen, phosphate, and potash were estimated from the results of over 1,000 experiments conducted in British Colonial and Commonwealth territories since about 1930. The responses (in terms of sugar) were examined in relation to ecological regions within each territory. Responses to organic manures, by-products, and lime were also summarized.

Nitrogen responses were observed everywhere. Under irrigation they were usually larger, while the ratoons generally responded more than the plant-canes. No residual response was observed. The sugar percentage was consistently reduced. Sulphate of ammonia appears to be the most effective form of nitrogen fertilizer.

With phosphate, the responses tended to be associated with soil types. They were generally rather small, and similar with successive crops. The effect on the sugar percentage was small and irregular.

Responses to potash were also associated with soil types and to some extent with rainfall. The ratoons tended to give somewhat higher responses than the plant-canes. Potash usually increased the sugar percentage.

Small, positive interactions were found between nitrogen and phosphate and between nitrogen and potash. Pen manure tended to reduce the responses to the main inorganic fertilizers. There was no evidence for interactions between fertilizers and varieties.

In order to gain a general picture of the responses of sugar-cane to fertilizers, all the available results of fertilizer experiments conducted since about 1930 in British Colonial and Commonwealth territories have been examined and summarized. The results of experiments with sugar-cane during the period 1900–40 have already been summarized by Carey and Robinson [1]. Similar summaries have been made by Crowther and Yates [2] for temperate crops, and recently by Yates, Finney, and Panse [3] for food grains in India. The present investigation revises and extends the work of Carey and Robinson by confining attention to experiments of modern randomized design, many of which were laid down within the past 10 years and with newer varieties; by examining the responses in relation to ecological regions within each territory and by giving them in terms of sugar. The analysis of these data has been carried out under a Colonial Development and Welfare Scheme.

Much of this information on the effects of fertilizers on sugar-cane already exists in qualitative form, but this summary collates the results and provides a sound, quantitative basis for determining a general fertilizer policy which will ensure the most efficient use of fertilizers in reaching and maintaining a high standard of production. For advisory purposes the results, which are average responses for fairly broad regions, will require modification in the light of local knowledge and experience, and especially of the results of soil or foliar analyses. Special care will be required in applying the results to small cane farms, since their history

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and practices are often very different from those of the large farms and estates on which most of the experiments were carried out.

Data Examined

In preparing this summary the results of over 1,000 experiments involving more than 2,000 crops were examined. Very few experiments were rejected because of the use of systematic designs, although there was some uncertainty about some of the South African experiments, of which few details of design were given. The numbers of experiments from the different countries are shown in Table 1. For each experiment the data included the yield of cane and particulars of the site or soil type; in some cases one or more additional items of information were

TABLE 1. *Classification of the Experiments*

Country	*No. of expts.*	*No. of crops*	*Design of experiment*	*No. of expts.*
Jamaica	242	417	Factorial	467
St. Kitts	148	232	Single Factor	399
Antigua	78	130	Miscellaneous	207
Barbados	51	81	..	..
Trinidad	140	309		
British Guiana	136	342	*Type of experiment*	
Mauritius	38	126	Plant-canes only	406
South Africa	83	146	Repeated	432
Queensland	157	237	Residual	84
			Ratoon	128
Total	1,073	2,020	Mixed	23

Time-distribution of the Experiments

Before 1940	507
1940–6	301
Since 1946	265

given such as yield of sugar or sucrose, variety of cane, basal manuring, results of soil analyses, age of cane at harvest, and rainfall during the crop season.

Usually the yields were published irrespective of significant effects, but in South Africa and Queensland there was a tendency to omit small responses. In so far as this is the case, the mean responses will be over-estimated. No data after 1947 have been used in the analysis for Queensland because the few results quoted could not be regarded as representative.

In many of the countries, much of the work on response to fertilizers was done before the war, using mainly single-factor experiments, or non-factorial designs when two or more factors were involved. Since 1940 the more comprehensive and accurate experiments have employed standard factorial designs [4], and these designs have been used increasingly in most of the territories. There have been relatively few experiments since the war. Jamaica, however, is exceptional for the large number (about 160) carried out between 1947 and 1952.

A notable development within the period under review has been the use of co-ordinated series of reliable and efficient factorial experiments well distributed over the main ecological regions. The first major series was carried out on commercial cane-farms in Queensland before the war. More recently, most of the results from Jamaica were obtained in this way while there have also been small but useful series in Mauritius, Barbados, and Antigua.

The different ways in which the successive crops can be treated enable the experiments to be divided into three main types, as distinguished by Carey and Robinson [1] and Hodnett [5]. Table 1 gives the numbers of each type. Experiments giving results for plant-cane only were enumerated separately. About 40 per cent. were of this type while rather more were continued either with fresh applications of the fertilizer treatments ('repeated' trials) or without further applications of fertilizers ('residual' trials) for one or more ratoon crops; sometimes fourth or higher ratoon crops were included while a few of the experiments were replanted. Experiments started on ratoon crops ('ratoon' trials) were carried out in all territories, whereas the smaller number of 'residual' trials were mainly in the Leeward Islands (Antigua and St. Kitts), Trinidad, and South Africa. Experiments of 'mixed' type were mostly with a single fertilizer.

Fertilizers

In almost all the countries, responses to nitrogen have received most attention while rather less work has been done with phosphate and potash. Table 2 gives the numbers of experiments with the main fertilizers used, together with the average and maximum rates of application of nutrient (N, P_2O_5, K_2O). A few experiments (eight in all) with double or triple superphosphate were also included under superphosphate. Alternative forms of fertilizer were tested in some of the experiments, usually against the standard forms on the basis of equal quantities of nutrient(s). The amounts of nitrogen and potash applied in these experiments were roughly the same as the averages for the respective territories. Experiments with organic manures, by-products, lime, and mulching are also shown in Table 2. In experiments of non-factorial design, the fertilizers were usually tested in the presence of adequate amounts of the other principal fertilizers; in some experiments basal dressings of pen manure were given at planting.

Effect of Fertilizers on Sugar Content

When examining the responses of sugar-cane to fertilizers the effect of the treatments on the sugar percentage must be considered. Table 3 shows the average changes in sugar percentage produced by the standard dressing of nutrient (50 lb. per acre) and also the numbers of crops on which the results were based. Nitrogen had a depressing effect everywhere, while potash increased the sugar percentage; the effect of phosphate was generally small and irregular. In most cases the change in the sugar percentage was approximately proportional to the rate of application of nutrient. The changes were standardized accordingly, mostly by means of linear regressions. In British Guiana, however, the data from

TABLE 2. *Fertilizers: Rates of Application and Numbers of Experiments*

Fertilizer	*Country*	*Rates of application*		*No. of expts.*
		*Average**	*Maximum*	
		Nutrient: lb. per acre		
Sulphate of ammonia (S/A) (20·5% N)	Jamaica	100	280	200
	St. Kitts	75	190	54
	Antigua	90	350	70
	Barbados†	80	225	38
	Trinidad	80	290	83
	British Guiana	110	240	64
	Mauritius	67	145	27
	South Africa	80	250	57
	Queensland	55	120	132
Superphosphate (18% P_2O_5)	Jamaica†	100	320	149
	St. Kitts	20	120	34
	Antigua†	50	180	46
	Barbados†	60	180	11
	Trinidad	60	180	51
	British Guiana	90	220	23
	Mauritius‡	60	200	30
	South Africa	100	300	62
	Queensland	50	130	117
Muriate of potash (60% K_2O) or Sulphate of potash (50% K_2O)	Jamaica	95	270	154
	St. Kitts	100	200	59
	Antigua	110	135	22
	Barbados	95	135	20
	Trinidad†	110	300	25
	British Guiana	130	360	20
	Mauritius	110	210	27
	South Africa	180	400	34
	Queensland	95	200	120
Alternative forms of fertilizers				
Nitrate of soda (N/S)		90	140	52
Ammonium nitrate		80	120	14
Cyanamide		90	115	26
Nitrochalk		100	140	15
Mixture (1 : 1 N/S and S/A)		100	115	12
Whale meal (10% N)		50	70	8
Ammonium phosphate (18% N, 18% P_2O_5)		60	140	21
Rock phosphate (34% P_2O_5)		200	680	17
Basic slag (17% P_2O_5)		100	300	25
Muriate of potash		110	110	6
Other treatments		*tons per acre*		
Pen manure		20	35	32
Filter press mud		10	30	18
Molasses		6	12	12
Dunder		20	30	3
Cotton seed meal		0·33	0·54	9
Bat guano		0·15	0·20	5
Lime§ low and high rates		2, 15	30	67
Mulch: inches		3″	6″	14

* Excluding the zero level.
† Excluding two experiments in each case with excessively high dressings.
‡ Including twenty-four experiments with phosphatic guano (24% P_2O_5).
§ Mainly ground limestone.

two sets of five experiments indicated that with nitrogen there was little reduction in the sugar percentage (−0·02 per cent.) over the range 0–50 lb. N per acre, but that at higher levels the effect was considerably greater; this is reflected in the larger value (−0·11 per cent.) obtained by taking the reduction to be proportional to the levels of application of nitrogen.

The effects of nitrogen and potash tended to be associated with the magnitude of the cane-yield responses, being more marked with the larger responses. Using data from Jamaica, the regressions of the change in sugar percentage on the cane-yield response were found to be significant, although the data were subject to considerable variation. The

TABLE 3. *Effects of Fertilizers on the Sugar Percentage*

Changes in sugar percentage produced by the standard dressing of 50 lb. per acre

	*Nitrogen** (N)	*Phosphate*† (P_2O_5)	*Potash*‡ (K_2O)
Jamaica	−0·14±0·02 (258)	−0·04±0·02 (197)	+0·06±0·02 (200)
St. Kitts	−0·08±0·06 (10)	+0·07±0·32 (9)	..
Antigua	−0·10±0·03 (16)	−0·09±0·04 (16)	..
Barbados	−0·04±0·02 (38)	−0·02±0·03 (8)	+0·06±0·02 (19)
Trinidad	−0·15±0·04 (66)	−0·08±0·04 (57)	+0·06±0·02 (55)
British Guiana	−0·02 (30) −0·11‖ ±0·02 (56)	+0·05±0·05 (40)	+0·04±0·02 (16)
Mauritius§	−0·12 (80)	+0·04 (80)	+0·02 (80)
South Africa	−0·03±0·02 (55)	0·00±0·02 (57)	+0·02±0·02 (21)
Queensland	−0·13±0·04 (192)	−0·02±0·04 (164)	0·00±0·02 (167)

* As sulphate of ammonia. † Mainly as superphosphate.
‡ As muriate or sulphate of potash. § Composite samples.
‖ Assuming change proportional to level of fertilizer application over the whole range of applications.

changes in sugar percentage per unit change in cane-yield response were −0·010±0·004 and +0·033±0·005 for nitrogen and potash, while the mean cane-yield responses were 3·7 and 2·1 tons per acre respectively. An association of this type was not observed, however, with the data from Queensland.

Response Curves and Standard Responses

Before combining the information from experiments using different numbers of levels and different rates of application of fertilizer, it was necessary to estimate the responses to a standard dressing of nutrient. Fifty lb. per acre was chosen as a convenient value although it is somewhat lower than the average dressings tested in most territories (Table 2). This standardization was effected by means of response curves of the same form as those used in similar summaries of experimental data [1, 2, 3]:

$$y = y_o + d\,(1 - 10^{-kx})$$

where y is the yield per acre with a dressing of x lb. per acre, y_o is the yield with no fertilizer, d is the limiting response, and k is a positive constant which determines the curvature of the response curve. For the

three main nutrients (and pen manure), the relative response curves adopted were as follows:

	k: acres per lb.			*k: acres per ton pen manure*
	Nitrogen	*Phosphate*	*Potash*	
Cane . .	0·006	0·010	0·010	0·03
Sugar . .	0·008	0·010	0·008	..

The curves for cane were those used by Carey and Robinson [1] while the suggested curves for sugar reflect the effect of fertilizers on the sugar percentage. Examination of experiments with three or more levels of fertilizer application confirmed the general reliability of these values.

The responses to different dressings relative to the response to the standard dressing are given in Table 4. Details of the method used to

TABLE 4. *Relative Response Curves*

Dressing lb./acre	*k: acres per lb.*			
	0·004	*0·006*	*0·008*	*0·010*
10 . .	0·24	0·26	0·28	0·30
20 . .	0·46	0·48	0·51	0·54
30 . .	0·65	0·68	0·70	0·73
40 . .	0·84	0·85	0·87	0·88
50 . .	1·00	1·00	1·00	1·00
60 . .	1·15	1·13	1·11	1·10
70 . .	1·29	1·24	1·20	1·17
80 . .	1·41	1·34	1·28	1·23
90 . .	1·53	1·43	1·34	1·28
100 . .	1·63	1·50	1·40	1·32
110 . .	1·73	1·57	1·44	1·35
120 . .	1·81	1·62	1·48	1·37
130 . .	1·89	1·67	1·51	1·39
140 . .	1·96	1·72	1·54	1·40
150 . .	2·03	1·75	1·56	1·42
160 . .	2·09	1·78	1·57	1·43
170 . .	2·14	1·81	1·59	1·43
180 . .	2·19	1·84	1·60	1·44
190 . .	2·24	1·86	1·61	1·44
200 . .	2·28	1·88	1·62	1·45
210 . .	2·32	1·90	1·63	1·45
220 . .	2·35	1·91	1·63	1·45
230 . .	2·38	1·92	1·64	1·46
240 . .	2·41	1·93	1·64	1·46
250 . .	2·44	1·94	1·64	1·46

compute the standard responses in experiments with three or more levels of fertilizer are given by Hodnett [5]; for experiments with two levels only, the standard responses were obtained simply by dividing the actual by the appropriate relative responses. Conversely, having determined the mean standard responses, the expected responses to any other dressings can be readily obtained by means of the relative response curves. Thus, if a standard response to nitrogen is 7·1 cwt. sugar per acre, the

expected response to 70 and 140 lb. per acre N will be $7{\cdot}1 \times 1{\cdot}20 = 8{\cdot}5$ and $7{\cdot}1 \times 1{\cdot}54 = 10{\cdot}9$ cwt. sugar per acre respectively. If r_s is the standard response, v is the value per cwt. sugar, and c is the cost per pound of nutrient (including the cost of application and of handling the increased crop), the dressings giving the maximum financial return (optimal dressings) may be calculated from the following formulae, which are based on the response curves for sugar:

Nitrogen (N) and potash (K_2O) $\quad 23{\cdot}1 + \frac{1}{0{\cdot}008}\log\left(\frac{vr_s}{50c}\right)$

Phosphate (P_2O_5) . . . $\quad 22{\cdot}6 + \frac{1}{0{\cdot}010}\log\left(\frac{vr_s}{50c}\right)$

The standardized responses in tons of cane per acre were converted to hundredweights of sugar per acre using an average sugar percentage for each territory, derived mainly from the experimental data. The mean responses were corrected for changes in sugar percentage with increasing rates of fertilizer application. The corrections depended on the average change in sugar percentage produced by the standard dressing (Table 3) and on the general level of yield.

TABLE 5. *Standard Responses to Nitrogen in Terms of Sugar Estimated from Yields of Cane and Directly from Yields of Sugar. (Data from Jamaica)*

Standard dressing = 50 lb. N per acre to each crop
Upper figure: from yields of sugar. Response curve $k = 0{\cdot}008$ acres per lb.
Lower figure: from yields of cane. Response curve $k = 0{\cdot}006$ acres per lb.

	Cwt. sugar per acre		
	Plants	*1st ratoons*	*2nd ratoons*
Not irrigated . . .	7·0 7·2 (65)	11·0 9·5 (37)	7·7 6·1 (16)
Irrigated	10·6 10·0 (80)	15·4 14·2 (37)	18·8 15·1 (20)
Lateritic soils . . .	1·8 1·9 (10)	4·3 3·6 (6)	−1·9 −0·5 (3)

Where results were given in terms of sugar, the responses could have been analysed directly. Using experiments in Jamaica for which both yields of cane and sugar were given, both methods gave very similar values for the principal estimates of the mean responses to *nitrogen*, which has the greatest effect on the sugar percentage. These results are shown in Table 5. The slightly higher values of the responses estimated directly from yields of sugar may be due in part to a slight inconsistency in the two values of k used for the response curves. As expected, the agreement was not so good for the smaller ecological subdivisions (not shown) but this is of little consequence since such estimates based on only a few experiments must generally be treated with some reserve. As it was considered desirable to include the maximum number of experiments, the analysis was based on the cane responses.

The responses were classified according to ecological regions defined by soil type, rainfall or moisture relationships, altitude, irrigation, or a combination of these. Experiments with basal pen manure and green manure were examined separately.

The mean responses for the major groupings of the responses are shown in Tables 6, 10, and 11. Within these main classifications the differences were mostly small and not significant. The standard errors were derived from pooled estimates of variance of the standardized responses within all classifications used in the different territories and over all the crops, since there was no evidence of a change in the variability of the responses with the crop.

Responses to Nitrogen

Responses to nitrogen (Table 6) were observed in all the territories and on all soil types, although in South Africa, the Leeward Islands (St. Kitts and Antigua) and on the lateritic soils in Jamaica, they were rather small. In these areas the rainfall is rather low (*c.* 40 in. p.a.) and may be the limiting factor, but elsewhere, where rainfall appears to be adequate, there was no simple association between rainfall and response to nitrogen. In Trinidad, for example, where the responses were examined in relation to soil groups based on their moisture characteristics, the responses were very similar. In Mauritius and in St. Kitts there is a considerable variation in rainfall associated with altitude, but again the responses were very similar.

Other factors no doubt influence the response to nitrogen. Carey and Robinson [1] have noted that Barbados is exceptional in that the responses are higher on the low rainfall (40 in.) black soils than on the red soils where the rainfall is higher (70 in.). This may be due to the difference in the respective nitrogen contents of these soils (0·15 and 0·25 per cent.). Similarly, the low responses in Antigua may not be entirely due to the low rainfall, but may be affected by the alkaline nature of the soils [6]. The standard practice of flood-fallowing the Frontland soils in British Guiana reduces the response of the plant-canes, since it is known [7] to increase the supply of available nitrogen, while the response of the ratoons is enhanced.

Under irrigated conditions the responses in Jamaica were significantly higher than where irrigation was not practised, while in Mauritius and Queensland similar effects were observed. Since the water supply can be thus controlled, so can the growth and uptake of nitrogen. Furthermore, in areas where irrigation is practised, the growing and ripening conditions are often very good, as in parts of Jamaica and also Hawaii. Even where the rainfall is relatively high, irrigation was found to be beneficial and to increase the response to nitrogen. It appears, therefore, that the distribution of the supply of moisture is almost as important as the total quantity received. The very variable responses *within* the soil types in Barbados may be attributed to the irregular distribution of the rainfall.

The areas of low rainfall are often very fertile, not being highly leached. When irrigated they give high yields and may therefore have higher

nitrogen requirements. The higher-yielding new varieties (e.g. in Trinidad) also appear to respond more to nitrogen, but as varieties and fertilizers were not tested in the same experiments no definite conclusion can be reached. Direct comparisons were made, however, in a few experiments in Jamaica (Table 7), but these did not show any interaction between varieties and nitrogen. Long-term experiments in Trinidad do not indicate any trend in response to nitrogen which could account for the increased response in recent years, but it appears that new and improved methods of tillage were introduced at about the same time as the newer varieties [7].

TABLE 6. *Responses to Nitrogen in Repeated Trials*

Standard dressing = 50 lb. N per acre to each crop as sulphate of ammonia

	Sugar percentage	*Cwt. sugar per acre*			
		Plants	*1st ratoons*	*2nd ratoons*	*S.E.*(±)*
Jamaica	13	..	..	..	..
Not irrigated	..	7·1 (83)	10·1 (44)	8·4 (24)	7·8
Irrigated	..	10·5 (114)	13·2 (46)	15·7 (21)	10·3
Lateritic soils (not irrigated)	..	3·9 (20)	4·5 (11)	2·0 (4)	4·4
St. Kitts	12	3·5 (24)	22·8 (12)	..	6·6
Antigua	12	2·5 (58)	10·1 (17)	..	3·9
Soils of fair natural drainage	..	1·7 (30)	10·0 (7)	..	..
Soils of impeded drainage	..	3·3 (28)	10·2 (10)	..	..
Barbados	12	8·8 (27)	16·8 (15)	..	9·4
Black soils	..	10·6 (15)	18·5 (8)	..	..
Red soils	..	6·5 (12)	14·8 (7)	..	..
Trinidad	11	10·8 (33)	8·8 (30)	10·4 (17)	6·9
Old varieties	..	8·5 (18)	8·2 (25)	9·6 (13)	..
New varieties	..	13·5 (15)	11·7 (5)	12·8 (4)	..
British Guiana	11	..	..	..	6·7
Unflooded Frontland	..	11·4 (5)	9·5 (5)	..	..
Flood-fallowed Frontland	..	6·2 (20)	17·5 (22)	..	..
Pegasse	..	8·0 (21)	6·3 (17)	..	..
Mauritius†‡	13	..	..	..	4·8
Irrigated	..	6·6 (3)	18·4 (3)	24·1 (3)	..
Not irrigated	..	3·8 (10)	10·5 (10)	10·7 (8)	..
South Africa	12	3·1 (39)	7·8 (15)	10·4 (27)	7·1
Queensland†	15	..	..	..	7·0
Burdekin area	..	20·6 (12)	14·5 (2)	..	..
Remainder	..	5·6 (70)	14·6 (39)	20·6 (12)	..

* Standard errors of a single standard response for vertical comparisons.
† Commercial cane sugar. ‡ Basal pen manure.

The first ratoon responses were generally considerably greater than those of the preceding plant-canes, while the increased responses were usually maintained in second and later ratoon crops. These results are confirmed in Table 8 where the differences in the responses of successive crops in the same series are examined. (Since the yields on the same plots in successive years are correlated, the standard errors were obtained

TABLE 7. *Mean Standard Responses of Different Varieties (Jamaica, plant-canes)*

Standard dressing = 50 lb. of nutrient per acre *Sugar percentage = 13%*

Variety	*Cwt. sugar per acre*	
	Response of standard variety	*Difference*
	Nitrogen (N)	
Comparisons with B.34104		
B.3439	19·1	+1·7 ± 2·4 (8)
B.37172	19·4	+3·3 ± 6·2 (3)
BH.10(12)	22·4	+0·8 ± 3·4 (4)
POJ.2878	5·8	−1·4 (1)
Comparisons with B.3439		
B.37172	20·7	+2·0 ± 5·8 (3)
BH.10(12)	27·2	−4·0 ± 4·6 (4)
POJ.2878	−4·2	+7·6 (1)
	Potash (K_2O) (not irrigated)	
Comparisons with B.34104		
B.41227	1·7	+1·3 ± 2·3 (4)
B.42231	−0·2	+5·1 ± 2·0 (3)
B.4362	1·7	+0·9 ± 1·9 (4)
B.37161	7·4	−9·3 (1)

TABLE 8. *Responses to Nitrogen for Crops in the Same Series in Repeated Trials*

Standard dressing = 50 lb. N per acre to each crop as sulphate of ammonia

	Cwt. sugar per acre					
	Plants a	*1st ratoons b*	*Difference b–a S.E.*	*1st ratoons c*	*2nd ratoons d*	*Difference d–c S.E.*
Jamaica						
Not irrigated	6·8	9·7	+2·9 ± 1·0 (43)	10·7	7·7	−3·0 ± 1·3 (22)
Irrigated	11·2	12·8	+1·6 ± 1·2 (45)	15·4	15·7	+0·4 ± 2·5 (21)
Lateritic soils (not irrigated)	2·3	4·1	+1·9 ± 2·0 (11)	2·3	2·0	−0·3 ± 0·1 (4)
St. Kitts	2·6	22·8	+20·2 ± 2·3 (12)	..	..	..
Antigua	4·4	10·1	+5·7 ± 1·2 (17)	..	..	..
Barbados	9·2	16·8	+7·6 ± 3·0 (15)	..	..	..
Black soils	12·7	18·5	+5·8 ± 4·1 (8)	..	..	..
Red soils	5·3	14·8	+9·5 ± 4·3 (7)	..	..	..
Trinidad	10·4	11·6	+1·2 ± 2·4 (17)	12·2	11·2	−1·0 ± 1·4 (17)
British Guiana						
Unflooded Frontland	11·4	9·5	−1·9 ± 3·9 (5)	9·2	8·8	−0·4 ± 4·8 (2)
Flood-fallowed Frontland	6·2	16·7	+10·5 ± 1·9 (20)	17·4	17·1	−0·3 ± 1·7 (17)
Pegasse	8·2	6·3	−1·9 ± 2·1 (17)	6·3	5·5	−0·8 ± 1·9 (13)
Mauritius						
Irrigated	6·6	18·4	+11·8 ± 3·4 (3)	18·4	24·1	+5·7 ± 3·6 (3)
Not irrigated	3·8	10·5	+6·7 ± 1·9 (10)	11·0	10·7	−0·3 ± 2·2 (8)
South Africa	6·4	8·6	+2·2 ± 1·5 (12)	..	..	..
Queensland	4·4	14·2	+9·8 ± 1·1 (50)	15·2	22·0	+6·8 ± 1·3 (16)

from the variation of the *differences*, within the classifications used.) The unflooded Frontland and Pegasse soils in British Guiana are exceptional in that the responses tend to decrease; in Jamaica the rendzina soils behave similarly, whether irrigated or not. In ratoon trials (following uniformly treated plant-canes) the responses were generally somewhat lower than in repeated trials, the mean difference being 2·6 ± 0·9 cwt. sugar per acre.

The greater response of the ratoons may be due to one or more factors —a residual effect from nitrogen remaining in the soil, a change in the plants, e.g. better root development, or a change in the soil, e.g. loss of structure after the first crop. There was no evidence of a residual response, irrespective of the magnitude of the plant-cane response, as shown by the following residual trials:

	Cwt. sugar per acre	
	Plants	*1st ratoons*
Jamaica . . .	9·7	−1·8 (2)
Antigua . . .	0·2	0·5 (13)
Barbados . .	2·2	−0·1 (4)
Trinidad . .	7·0	−1·3 (10)
South Africa . .	−0·4	−2·9 (9)

These results, together with the rather lower response of ratoons in ratoon trials, suggest that the effect is more likely due to a combination of the latter factors.

TABLE 9. *Comparison of other forms of Nitrogen Fertilizer with Sulphate of Ammonia*

	Cwt. sugar per acre					
Country	*Nitrate of soda*	*Ammonium nitrate*	*Nitro-chalk*	*Cyan-amide*	*1 : 1 mixture N/S and S/A*	*Whale meal*
St. Kitts .	−2·2 (7) ± 0·9	−0·8 (7) ± 1·0	..	..	..	..
Antigua .	0·0 (5) ± 1·3	.. ..	.. ..	.. ..	.. ..	.. ..
Trinidad .	+0·9 (5)* ± 2·9	−1·7 (1) ..	.. ..	.. ..	.. ..	.. ..
British Guiana Flood-fallowed	−6·0 (9)	−0·5 (4)	+0·1 (7)	−2·3 (15)	−2·9 (6)	..
British Guiana Frontland	± 0·6	± 1·0	± 1·1	± 0·7	± 1·3	..
Pegasse .	−0·6 (10) ± 0·6	.. ..	−0·2 (5) ± 1·3	+0·2 (8) ± 0·9	−0·2 (5) ± 1·4	.. ..
South Africa	−0·3 (8) ± 1·6	.. ..	+0·5 (3) ± 0·6	.. ..	.. ..	−0·2 (8) ± 1·9

* Plant-canes only.

The effect of varying the time of application of nitrogen from planting up to 12 weeks afterwards was investigated in seven experiments in Jamaica. There was no evidence to suggest that application after planting would give a larger increase in yield. There was also no evidence in favour of splitting the application.

Table 9 shows the differences (averaged over all crops in the

experiments) in the standardized responses to alternative forms of nitrogenous fertilizers. Sulphate of ammonia and nitrochalk appear to be the most effective, ammonium nitrate, cyanamide, and nitrate of soda giving somewhat smaller responses. As the sugar percentages were very similar, no correction to the differences was required.

Responses to Phosphate

Table 10 shows that the responses to phosphate were mostly rather small and very similar with successive crops. There was, however, a

TABLE 10. *Responses to Phosphate in Repeated Trials*

Standard dressing = 50 lb. P_2O_5 per acre to each crop mainly as superphosphate

	Sugar percentage	Cwt. sugar per acre			
		Plants	1st ratoons	2nd ratoons	S.E.*(±)
Jamaica	13	2·2 (139)	2·5 (80)	2·1 (44)	..
River alluvium and marine clay	..	1·9 (60)	2·0 (34)	1·4 (22)	6·1
Inland Basin soils	..	2·9 (58)	3·3 (37)	3·0 (18)	5·3
Rendzina, tuffs, shales, and conglomerates	..	1·3 (21)	0·9 (9)	1·6 (4)	4·4
St. Kitts	12	3·0 (19)	4·0 (8)	..	5·8
Lower lands	..	−4·4 (4)	1·8 (3)	..	..
Middle lands	..	1·8 (6)	5·0 (2)	..	..
Upper lands	..	7·0 (9)	5·6 (3)	..	..
Antigua	12	2·0 (36)	2·4 (17)	..	3·1
Barbados	12	0·4 (10)	3·0 (4)	..	1·7
Trinidad†	11	3·9 (48)	3·3 (27)	4·5 (9)	4·2
Old varieties	..	2·7 (36)	2·9 (25)	4·2 (8)	..
New varieties	..	7·7 (12)	8·4 (2)	7·0 (1)	..
British Guiana	11	2·2 (22)	2·1 (15)	3·8 (9)	4·5
Frontland	..	1·3 (16)	1·1 (12)	2·6 (8)	..
Pegasse	..	4·6 (6)	5·9 (3)	13·1 (1)	..
Mauritius‡	13	−0·1 (17)	0·3 (17)	1·4 (16)	3·5
Medium and low rainfall	..	−1·3 (11)	−1·1 (11)	0·5 (11)	..
High rainfall	..	2·0 (6)	2·9 (6)	3·3 (5)	..
South Africa	12	..	..	..	7·4
Alluvial and clay soils	..	2·4 (17)	2·7 (3)	..	..
Loams and sands	..	9·3 (33)	6·8 (6)	..	..
Queensland	15	..	..	..	7·9
Alluvial and volcanic loams	..	4·5 (51)	2·1 (29)	2·1 (12)	..
Schists and sandy/gravelly loams	..	8·6 (43)	8·2 (21)	7·4 (8)	..

* Standard errors of a single standard response for vertical comparisons.

† Excluding experiments on soils with a perrenial supply of subsoil seepage water, where no response was observed.

‡ Phosphatic guano.

closer association with soil type than in the case of nitrogen, which was shown most clearly in South Africa and Queensland, where the more substantial responses were obtained. In British Guiana the Pegasse soils gave responses to all forms of phosphate, whereas on the Frontland soils there was generally very little response, although in both cases there was considerable variation from site to site. The more responsive areas in Jamaica were on the Inland Basin soils, where in the region of medium rainfall six unirrigated experiments which had abnormally low mean yields gave an average response over all crops of 7·0 cwt. sugar per acre. As with nitrogen, the newer varieties responded considerably more to phosphate than the old, but unfortunately no direct comparisons were made.

The available phosphate in the top-soil was recorded for fourteen of the experimental sites in Trinidad. Where there was less than 30 p.p.m. P_2O_5 (Truog) the responses were clearly greater than where the available phosphate exceeded this value. The average responses over all crops were respectively 4·0 and 1·3 cwt. sugar per acre.

There is also some evidence of an association with rainfall, areas of high rainfall with consequently greater leaching being rather more responsive. In the wetter northern district in Queensland, for example, the average response was 7·2 compared with 2·2 cwt. sugar per acre in the drier districts to the south, these values being free from the effects of the soil types in these areas. Similarly, the responses on the upper lands in Mauritius and St. Kitts also tended to be somewhat higher.

The responses of successive crops appear to be very similar. Examination of the differences between crops in the same series in the same way as for nitrogen showed only slight and non-significant changes. Nevertheless, there may be a considerable residual effect, especially when the plant-cane response is large, as indicated by the following results of residual trials:

	Cwt. sugar per acre	
	Plants	*1st ratoons*
St. Kitts . . .	4·1	7·0 (5)
Trinidad . . .	2·5	1·8 (5)
British Guiana		
Frontland . .	−0·5	1·8 (10)
Pegasse . .	6·9	6·1 (7)
South Africa		
Alluvial and clays .	0·8	1·6 (7)
Loams and sands .	13·4	8·4 (7)

Where there is no large direct response it appears, however, from Table 10 that some phosphate may be required, but owing to the residual effect one dressing at planting may be sufficient for the series. In all cases, the question of the distribution of the fertilizer over the crops in the series requires further investigation.

From the few experiments using alternative phosphatic fertilizers,

there do not appear to be any appreciable differences; most of these were in British Guiana. The only direct comparisons were as follows:

	Mean response of all crops cwt. sugar per acre	
Trinidad		
Ammonium phosphate	0·1	(5)
Superphosphate + nitrogen	2·1	
British Guiana		
Basic slag	5·1	(3)
Superphosphate	5·1	
Ammonium phosphate	5·0	(5)
Basic slag + nitrogen	4·0	

Responses to Potash

Table 11 shows that in most areas some response to potash was observed. As with phosphate there was considerable association with soil

TABLE 11. *Responses to Potash in Repeated Trials*

Standard dressing = 50 lb. K_2O per acre

	Sugar percentage	*Cwt. sugar per acre*			
		Plants	*1st ratoons*	*2nd ratoons*	*S.E.*(±)*
Jamaica	13	5·5 (155)	7·7 (81)	6·6 (41)	..
River alluvium and marine clay	..	3·1 (65)	3·6 (35)	2·7 (20)	5·7
Inland Basin alluvium	..	8·7 (70)	12·5 (37)	12·1 (17)	7·8
Rendzina, tuffs, shales, and conglomerates	..	2·3 (20)	3·6 (9)	2·7 (4)	3·4
St. Kitts	12	5·0 (37)	5·2 (20)	..	3·4
Lower lands	..	3·3 (12)	4·3 (7)	..	..
Middle lands	..	5·6 (8)	4·3 (4)	..	..
Upper lands	..	5·9 (17)	6·2 (9)	..	..
Antigua	12	1·6 (18)	0·9 (7)	..	1·0
Barbados	12	3·4 (21)	7·1 (9)	..	5·1
Black soils	..	1·6 (13)	7·7 (5)	..	..
Red soils	..	6·2 (8)	6·4 (4)	..	..
Trinidad	11	5·0 (51)†	4·7 (33)†	5·2 (11)†	3·6
Less than 80 p.p.m. K_2O	..	8·0 (22)	6·4 (17)	7·3 (7)	3·1
Over 80 p.p.m. K_2O	..	2·0 (12)	2·5 (9)	1·6 (3)	
British Guiana	11	3·4 (17)	2·5 (13)	3·0 (13)	3·6
Mauritius	13	2·1 (17)	2·5 (17)	2·2 (16)	2·9
Lower rainfall	..	1·1 (4)	3·2 (4)	1·5 (4)	..
Medium and high rainfall	..	2·4 (13)	2·3 (13)	2·4 (12)	..
South Africa	12	..	..	..	5·4
Alluvial and clay soils	..	6·8 (11)	11·5 (3)	..	..
Loams and sands	..	2·2 (14)	2·5 (6)	..	..
Queensland	15	..	..	..	6·0
Schists and volcanic loams	..	9·2 (32)	8·0 (14)	6·8 (10)	..
Alluvial and sandy/gravelly loams	..	3·2 (64)	2·8 (36)	7·5 (11)	..

* Standard errors of a single standard response for vertical comparisons.

† Including other experiments for which soil analyses were not available.

types and the results of soil analysis. The Inland Basin soils in Jamaica and the volcanic loams in Queensland are known to be deficient in potash, while on the alluvial and clay soils in South Africa there were also substantial responses.

In some cases, the higher responses were in areas of heavier rainfall. The schist soils in Queensland, for example, occur only in the wetter Northern district, while in Jamaica on the river alluvial soils under high rainfall conditions the average response in twenty-five experiments (5·3 cwt. sugar per acre) was significantly greater than in the drier areas

TABLE 12. *Responses to Potash in the Same Series in Repeated Trials*

Standard dressing = 50 lb. K_2O per acre

	Cwt. sugar per acre							
	Plants a	*1st ratoons b*	*Difference*		*1st ratoons c*	*2nd ratoons d*	*Difference*	
			b–a	*S.E.*			*d–c*	*S.E.*
Jamaica								
Not irrigated	7·0	9·6	+2·6	±1·3 (42)	9·5	10·3	+0·8	±0·7 (20)
Irrigated	1·5	3·0	+1·5	±0·8 (28)	1·9	1·5	−0·4	±1·4 (16)
Lateritic soils	10·6	13·1	+2·5	±2·8 (10)	17·6	12·2	−5·4	(3)
St. Kitts	5·4	5·2	−0·2	±0·9 (20)	..	..	..	..
Antigua	1·7	0·9	−0·8	±0·4 (7)	..	..	..	..
Barbados	2·2	7·1	+4·9	±2·7 (9)	..	..	..	..
Black soils	0·5	7·7	+7·2	±3·6 (5)	..	..	..	..
Red soils	4·3	6·4	+2·1	±4·0 (4)	..	..	..	..
Trinidad								
Less than 80 p.p.m. K_2O	8·0	6·4	−1·6	±0·8 (17)	6·2	7·3	+1·1	±0·7 (7)
Over 80 p.p.m. K_2O	2·0	2·7	+0·7	±1·1 (8)	2·8	1·6	−1·2	±1·1 (3)
British Guiana	3·1	2·4	−0·7	±1·9 (10)	2·4	2·7	+0·3	±1·1 (9)
Mauritius	2·1	2·5	+0·4	±0·4 (17)	2·3	2·1	−0·2	±0·6 (16)
South Africa								
Alluvial and clays	11·2	16·4	+5·2	±3·5 (2)	..	..	..	..
Loams and sands	0·9	−0·7	−1·6	±2·9 (3)	..	..	..	..
Queensland	3·7	4·6	+0·9	±0·5 (43)	5·9	6·4	+0·5	±0·9 (15)

under irrigation where the average plant-cane response in twenty-six experiments was 1·3 cwt. sugar per acre. Similar effects were observed in Barbados and on the higher lands in Mauritius and St. Kitts.

There does not appear to be any marked interaction with varieties (Table 7). The difference approaching significance was observed when the standard variety did not respond to potash manuring.

The differences between successive crops in the same series are shown in Table 12. The ratoons tended to respond rather more than the plant canes, especially when the direct responses were large. In discussing the responses of successive crops the residual effect must also be

considered. This effect, however, appears to be small, as indicated by the following fragmentary data:

	Cwt. sugar per acre	
	Plants	*1st ratoons*
Barbados . .	4·7	2·2 (6)
Trinidad . .	6·1	1·8 (2)
British Guiana . .	4·7	2·0 (2)
South Africa		
Alluvial and clays .	6·9	0·7 (5)
Loams and sands .	0·6	0·5 (2)

In most territories both sulphate and muriate of potash were used. As they appear to be equally effective all experiments were grouped together. In one set of five experiments in British Guiana a direct comparison was made; with both forms the average response was 2·2 cwt. sugar per acre.

Interactions

In spite of the considerable number of factorial experiments, very little data was available on the interactions between the main plant nutrients. The standardized values given in Table 13 are based on means of all

TABLE 13. *Interactions**

	Cwt. sugar per acre		
	NP	NK	PK
Jamaica . .	+0·23±0·70 (11)	+0·16±0·65 (11)	−0·52±1·38 (11)
St. Kitts . .	..	..	+0·12±1·42 (12)
Antigua . .	+0·34±0·31 (28)	+0·43±0·22 (11)	−0·14±0·36 (15)
Barbados . .	+0·53±0·86 (9)	+0·38±0·36 (18)	+0·26±0·50 (7)
Trinidad . .	+0·59±1·03 (3)	+1·03±0·68 (4)	−0·07±0·44 (23)
Mauritius . .	+0·60±0·49 (21)	−0·13±0·52 (20)	0·00±0·47 (21)
South Africa .	+0·53±0·34 (3)	+0·77±2·14 (4)	−0·48±0·36 (2)

* As defined by Yates [4].

the crops in the experiments. Although there was considerable variation, the NP and NK interactions are quite consistent. Crowther and Yates [2] report similar interactions with sugar-beet. The magnitudes of these effects are, however, small (+0·5 and +0·4 cwt. sugar per acre respectively), and so will be of no great importance in practice. There does not appear to be any interaction between phosphate and potash.

If, for example, the main effects of nitrogen and phosphate are 10·2 and 3·8 cwt. sugar per acre respectively, the response to nitrogen in the presence of phosphate will then be 10·2+0·5 = 10·7 cwt. per acre; in the absence of phosphate it will be 9·7 cwt. per acre, i.e. the presence of phosphate increases the response to nitrogen by 1 cwt. per acre. If it is decided to apply both nitrogen and phosphate, the difference in yield between a treated and an untreated area will be 10·2+3·8 = 14·0 cwt.

per acre, i.e. the average response to both fertilizers together does not depend on the interaction, but only on the main effects.

Responses to Organic Manures and other Treatments

The small number of experiments with pen manure are summarized in Table 14, together with the effect of pen manure on the responses to

TABLE 14. *Responses to Pen Manure and Responses to Nitrogen, Phosphate, and Potash in the presence and absence of Pen Manure (P.M.) and Green Manure (G.M.)*

		Cwt. sugar per acre		
		Plants	*1st ratoons*	*2nd ratoons*
Pen manure: 15 tons per acre				
St. Kitts		7·5 (3)	9·7 (2)	..
Antigua		10·6 (10)	8·5 (7)	6·1 (3)
Barbados		9·8 (3)	2·5 (3)	..
Trinidad		10·4 (15)	3·8 (13)	2·1 (6)
Nitrogen: 50 lb. N per acre				
St. Kitts	—	3·5 (24)	22·8 (12)	15·7* (6)
	P.M.	2·9 (7)	13·6 (2)	7·9* (3)
Antigua	—	3·7 } (5)	8·9 } (2)	..
	P.M.	4·6 }	7·9 }	
Trinidad	—	9·2 } (4)	11·9 } (3)	6·6 } (1)
	P.M.	6·1 }	11·0 }	1·6 }
Mauritius	—	7·8 (6)	13·0 (6)	21·7 (5)
	P.M.	3·8 (10)	10·5 (10)	10·7 (8)
Queensland (exc. Burdekin)	—	5·6 (70)	14·6 (39)	20·6 (12)
	G.M.	3·3 (28)	15·6 (16)	21·5 (9)
Phosphate: 50 lb. P_2O_5 per acre				
St. Kitts	—	3·0 (19)	..	..
	P.M.	1·1 (2)	..	..
Antigua	—	2·8 } (5)	1·3 } (2)	..
	P.M.	1·4 }	1·7 }	
Trinidad	—	2·0 } (5)	4·4 } (5)	..
	P.M.	2·1 }	2·9 }	
Mauritius	—	0·4 (6)	−0·4 (6)	2·0 (6)
	P.M.	0·1 (7)	2·1 (7)	1·3 (6)
Queensland	—	6·7 (68)	5·7 (37)	4·5 (13)
	G.M.	5·6 (26)	1·7 (13)	3·6 (7)
Potash: 50 lb. K_2O per acre				
St. Kitts	—	5·0 (37)	5·2 (20)	2·8*(8)
	P.M.	1·3 (8)	0·5 (1)	0·3*(3)
Antigua	—	2·0 } (3)	1·7 } (2)	..
	P.M.	3·2 }	0·9 }	
Trinidad	—	6·6 } (6)	6·4 } (6)	4·9 } (2)
	P.M.	3·3 }	4·1 }	2·8 }
Mauritius	—	3·7 (6)	1·6 (6)	2·0 (6)
	P.M.	1·2 (7)	2·9 (7)	2·7 (6)
Queensland	—	5·0 (68)	4·2 (35)	6·7 (11)
	G.M.	5·7 (28)	4·3 (15)	7·7 (10)

* Ratoon trials.

the inorganic fertilizers. Pen manure gave good responses with a considerable residual effect which may persist for a number of years [5].

Comparisons of the responses to nitrogen, phosphate, and potash in the presence and absence of pen manure were made in the same experiments

only in Antigua and Trinidad; elsewhere a basal dressing of pen manure was given at planting in some of the experiments. Since pen manure supplies varying amounts of nitrogen, phosphate, and potash, it may be

TABLE 15. *Responses to Various Fertilizer Treatments, Lime, and Mulching*

	Cwt. sugar per acre		
	Plants	*1st ratoons*	*2nd ratoons*
Filter press mud (3% P_2O_5): 50 lb. P_2O_5 per acre			
Jamaica	5·2 (3)	4·4 (3)	5·1 (3)
St. Kitts	4·0 (4)	1·8 (2)	..
Antigua	4·1 (2)	9·2 (2)	6·5 (1)
Trinidad	1·8 (6)	3·5 (2)	2·2 (1)
South Africa	21·0 (3)	..	..
Molasses (2½% K_2O): 50 lb. K_2O per acre			
Jamaica	2·0 (2)	..	..
St. Kitts	1·5 (2)	3·9 (1)	..
Trinidad	7·5 (3)	3·1 (2)	1·1 (1)
South Africa	5·4 (1)	..	..
Queensland	18·5 (3)	17·3 (3)	9·2 (1)
Dunder (0·6% K_2O): 50 lb. K_2O per acre			
Jamaica	9·4 (3)	8·5 (3)	4·4 (2)
Cotton seed meal: 750 lb. per acre			
St. Kitts	3·2 (9)	1·5 (1)	..
Bat guano: 3 cwt. per acre			
Jamaica	6·5* (5)	..	..
Lime‡: *tons per acre*			
Jamaica 3–30	6·0† (8)	..	..
St. Kitts 3	2·0 (6)	−1·9 (3)	..
Barbados 2	−4·2 (2)	..	..
Trinidad 5–30	10·3 (4)	9·1 (4)	8·5 (4)
Residual 2nd series	7·6 (3)	6·5 (3)	7·7 (2)
Residual 4th series	3·7 (2)	6·3 (2)	..
0–1	2·0 (3)	0·2 (2)	..
British Guiana 1	2·1 (26)	0·6 (25)	0·7 (22)
5	5·2 (12)	2·5 (9)	4·2 (8)
South Africa 2½	0·8 (5)	..	..
Mulch: 3 inches			
Jamaica	7·1 (4)	3·4 (3)	−0·7 (2)
St. Kitts	8·1 (7)	2·3 (7)	−1·4 (2)
Trinidad	6·3 (3)	4·8 (3)	5·6 (3)

* Plants and ratoons. † Maximum. ‡ Mainly ground limestone.

expected to reduce the responses to the inorganic fertilizers. This was usually the case, the effect being most pronounced with the plant-canes. With phosphate and potash the difference in response was also influenced by the nutrient status of the soil. For example, the comparisons in Trinidad were made in two long-term experiments on a soil deficient in potash

but not in available phosphate. In Queensland, green manure tends to cause a slight reduction in the responses, but does not appear to have much residual effect.

The effects of by-products, other organic fertilizers, lime, and of mulching with bagasse are shown in Table 15. Most of these treatments were applied only at planting, and frequently produced good responses with considerable residual effects. Filter-press mud has been suggested by Chinloy, Innes, and Finney [8] to be a satisfactory alternative to superphosphate in Jamaica, while it has also been recommended in Trinidad for sites deficient in readily available phosphate [9]. There were good responses also to molasses and dunder, which supply mainly potash. Mulching appears to have a beneficial effect which may persist for the second crop. Responses to liming were very variable, but the higher dressings usually gave not only larger immediate responses but also effects which may last for the remainder of the crop series; indeed, long-term experiments in Trinidad, involving replantings, have shown that a marked effect may remain 10 years or more after the lime was applied. Nine experiments in British Guiana showed no difference between ground limestone and slaked lime.

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SEASONALITY OF BEEF AND VEAL SUPPLIES IN THE UNITED KINGDOM

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Summary

This paper examines the seasonality of home-killed and imported beef and veal supplies in the United Kingdom before, during, and since the 1939–45 War. It is intended as the introduction to a series of papers which will deal with the various problems which seasonality poses and will suggest means whereby orderly supplies may be made available to the United Kingdom market.

It has long been recognized that the prices of agricultural products tend to fluctuate more widely than the prices of industrial products. Seasonality of supply is among the causes of this price instability. Those agricultural products such as grains which may be stored without loss of quality do not suffer from the effects of seasonal production as do the more perishable products. Livestock products generally are perishable and seasonality of production leads to realized prices being low in the periods of above-average production. Beef producers in particular suffer from the effects of seasonality because freezing to even out supplies causes loss of value in comparison with fresh meat. Chilling is not a satisfactory way of dealing with the seasonality because deterioration occurs after six weeks unless the meat is previously frozen down.

The production of beef and veal in the United Kingdom has been seasonal for many years. A report in 1929 [1] drew attention to the seasonal pattern of home production and the Fatstock Reorganization Commission reported in 1934 [2] that seasonality of home-produced beef was a cause of fluctuating producers' prices. These prices were obviously also influenced by the availability of imported beef. This paper deals with United Kingdom total supplies, home production and imports, of beef and veal. A second paper will study the seasonal pattern of production and of exports from Argentina, Australia, and New Zealand.

United Kingdom Supplies

Reliable data on United Kingdom total supplies before the war are lacking, because production of home-killed beef was merely estimated. The Ministry of Food estimated that the average home-killed production in the years 1936–9 was 615,000 tons a year. Imports in that period averaged 582,000 tons a year. Thus home production presumably accounted for about one-half of total supplies.

Sufficient data are not available to estimate the seasonality of total supplies immediately before the war. The evidence presented in the report of the Fatstock Reorganization Commission clearly shows that between 1927 and 1931 the peak supplies were available between

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October and January owing to the high level of home production in that period.

By 1945 supplies of beef and veal had decreased to 747,900 tons which was about 62 per cent. of the pre-war supplies. Home-killed production accounted for 73 per cent. of total supplies in 1945 compared with about half before the war. Supplies became more seasonal as the home-produced percentage increased.

After the war total supplies of beef increased until 1950, but did not attain the pre-war level. Imports increased from the low figure of 201,000 tons in 1945 to 508,300 tons in 1947, then fell each year until in 1952 only 130,600 tons were available. Home-killed production varied from year to year, but exceeded the estimated pre-war level in 1950 and 1951 when 630,400 and 645,600 tons were produced. In 1952 total supplies were only about 61 per cent. of those available pre-war, but in 1953 increased imports made total supply equal to about 77 per cent. of the pre-war level. Supplies in 1947 were almost equally divided between home-killed and imported, but by 1952 the home-killed proportion was 82 per cent. Detailed statistics of supplies are given in the Appendix.

United Kingdom Home Production

An analysis of the seasonal variation of production, on a partial sample of fat cattle sold for slaughter between 1934 and 1938 [3], supports the evidence available to the Fatstock Reorganization Commission for 1927–31. It would be fair to conclude that pre-war producers suffered from the autumnal glut. The Commonwealth Economic Committee's report on Meat [4] for 1938 shows the effect of the glut on beef prices during the autumn.

The annual production of beef and veal during the war was less than the pre-war average. This was partly due to the policy of not providing imported feeds for beef cattle and the ploughing up of grassland. There were fewer beef cattle in the country and because of a lower plane of feeding, fattening was slower. Home-killed production, which declined to 77 per cent. of the estimated pre-war level in 1942, had increased by 1945 to 89 per cent.

Between 1940 and 1945 the pattern of production was markedly seasonal, varying from an index[1] of 143·0 in October to 68·1 in December. The index was above 100 for the months of April to October with the exception of June, and below 100 for the months November to March. April production was almost entirely from yard-fed cattle. Grass-finished cattle accounted for the high level of production in October. The October sale of unfinished beasts, in preference to carrying them on for a few more weeks, aggravated the situation.

[1] The Index of Seasonal Variation is obtained by calculating the trend from the twelve-month moving average of the monthly production figures. The ratio of the actual production in each individual month to the trend figure for each month is obtained. The arithmetic mean of all the ratios for each month is calculated. A set of twelve figures is required varying around 100 as a mean, hence adding to 1,200. Each month's mean is adjusted therefore to ensure that the total is 1,200. The Index of Seasonal Variation is thus in ratio form.

In each of the years 1940–5 the guaranteed producer-prices varied seasonally, being highest in June and lowest in October. On the whole production was not influenced by this pattern of prices. The expected extra costs of producing for sale at times of high prices were greater than the expected extra receipts. Producers were, on the whole, prepared to accept lower prices. It would appear that the low level of production in the month of highest prices (June) was directly the result of the inability to get stores forward enough in the winter for June finishing.

The main feature in the contrast between the pre-war and wartime patterns of production is the wartime low level of production in December and January. Production before the war was well above the monthly average for the year in those months, whereas in the war years production in January and December was 16 per cent. and 32 per cent. below that monthly average. Another divergence between the two periods is the April peak in the war years (22½ per cent. above the average monthly production for the year). Both the Reorganization Commission's index for 1927–31 and Richardson's index [3] for 1934–8 showed that pre-war production in the spring months was below the annual average rate.

When the war ended, balance-of-payments problems dominated the post-war economy and many of the agricultural controls were retained. Beef production increased substantially and in 1950 and 1951 exceeded the pre-war level. The granting of special rations for fat cattle in the winters of 1949–50 and 1950–1 had the desired effect. The calf-rearing subsidies and higher prices for fat cattle were no doubt contributing factors in this expansion of production.

Post-war production has been of an increasingly seasonal pattern. It has varied from a trough in June to a peak in October as in the war years. In the last four years of control (1950–3) the trough in June became more pronounced. The October peak was not quite so high as it had been in the years 1946–9, but was 82 per cent. above the average monthly rate for the period. The autumnal glut is best described by noting that in 1953, 37 per cent. of the year's production was concentrated in the months August, September, and October. In contrast only 3 per cent. was produced in June and only 24 per cent. in the months December to March inclusive.

This irregularity of supply may be ascribed to the producers' continued belief that beef cattle finished off grass were less costly than those finished by any other method. The relatively lower guaranteed prices in the autumn were not sufficiently low to discourage autumn production.

Data on the changing seasonality of U.K. beef production from 1940 to 1953 are represented graphically in Fig. 1.

The outstanding feature of British beef production since 1940 has been its increasingly seasonal pattern. As a measure of this, the standard deviation may be used. The key to Fig. 1 also shows the standard deviation of monthly indices from the general average of 100, calculated for the series of data for 1940–5, 1946–9, and 1950–3.

This increasingly seasonal pattern of production is the more remarkable if it is remembered that the Ministry of Food guaranteed prices were weighted more and more heavily against autumn production. In

the early years of control the differential between June and October prices was eight shillings a hundredweight. By 1953 this modest difference had increased to thirty-seven shillings a hundredweight.

United Kingdom Imports

In the years 1936–8 the annual imports of beef and veal averaged 582,000 tons. Argentina was the principal supplier, sending about two-thirds of the total imports each year. Australia and New Zealand contributed two-thirds of the balance and Uruguay and Brazil most of the remainder. Argentine supplies were characterized by their regularity of

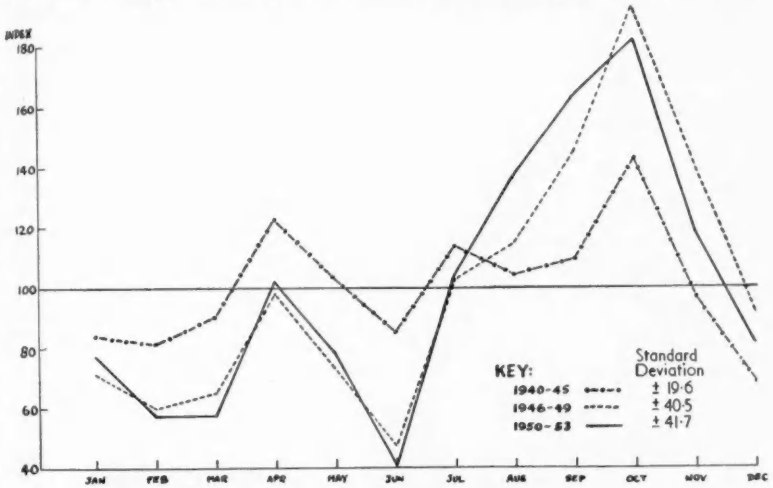

FIG. 1. Indices of the average monthly production of home-killed beef and veal in the United Kingdom for the years 1940–5, 1946–9, and 1950–3. (General monthly average = 100.)

arrival and by the high proportion of chilled beef. Most of the Australian and New Zealand supplies arrived between July and October.

On the whole the total supplies of imported beef before the war arrived regularly throughout the year. This was mainly due to the weighting of the Argentine shipments. The seasonality that did exist was caused by the Australian and New Zealand supplies.

During the war imports of beef and veal were drastically reduced. By 1945 only 35 per cent. of the pre-war tonnage was imported. Shortages of shipping and policy decisions were the main reasons for this decline. Chilled beef was entirely displaced by frozen beef because chilled beef might deteriorate seriously if delayed on the voyage. Secondly, chilled beef could not be held indefinitely in store to meet the exigencies of rationing.

Between 1941 and 1945 there were seasonal peaks in imports in April, July, and October which coincided with above-average home-killed production. Although imports in wartime were irregular because of ship-

ping losses, the seasonality which did occur resulted in longer periods of cold storage than would have been allowed before the war. The problem of dovetailing home production and imports was of minor importance compared with the need to safeguard the ration. With guaranteed prices for British production the arrivals of imports had no effect on the home prices.

Since 1945 imports of beef have varied greatly from year to year, being lowest in 1952 when 130,600 tons were available and highest in 1947 when 508,300 tons arrived. The quantity of post-war imports has been greatly influenced by the exportable surpluses from Argentina and Australia. For various reasons production in Argentina decreased. More-

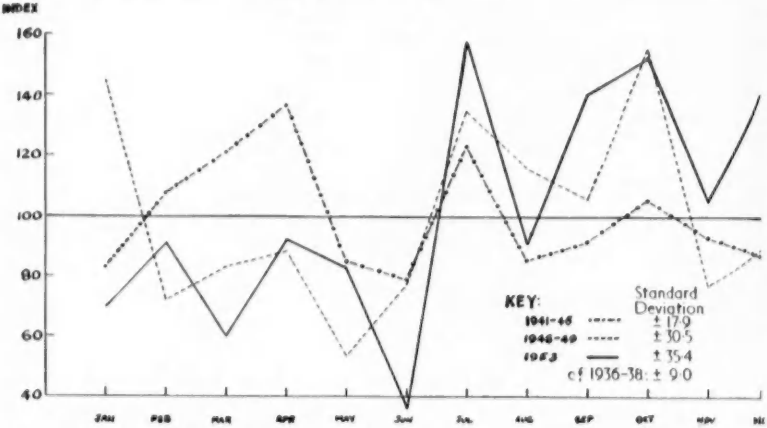

FIG. 2. Indices of the average monthly imports of beef and veal into the United Kingdom for the years 1941–5, 1946–9, and 1953. (General monthly average = 100.)

over, a rising internal population and a sustained high level of consumption, to say nothing of difficulties of negotiation, all played their part in decreasing imports of Argentine beef into the United Kingdom. Thus in 1951, only 48,000 tons of beef arrived from Argentina and in 1953 only 81,000 tons compared with 248,000 tons in 1947.

Australian beef exports have been affected by the high level of internal consumption brought about by the rising population and living standards. Another factor was drought in Queensland, particularly in 1952, when beef imports from Australia fell to 11,100 tons compared with 101,500 tons in 1947 and 135,900 tons in 1953. Queensland supplies the major proportion of Australian beef exports—the other states producing mainly for home consumption.

The seasonal pattern of imports is clearly seen in Fig. 2 which relates to the years 1941–5, 1946–9, and 1953.

Between 1946 and 1953 when United Kingdom home production was becoming more seasonal, the seasonal pattern of imports clashed with the home production, as shown by comparison of Fig. 1 and Fig. 2. Thus in

the month of October when home production was 70–80 per cent. above the monthly average for the year, imports were between 50 and 60 per cent. above this average. When the Ministry of Food was responsible for total supplies, the general body of taxpayers financed the storage of imported beef, while British producers' prices were protected from the impact of the seasonal imports.

Conclusion

Arrival of imported supplies at times when large quantities of home-killed supplies are available is expensive in terms of storage. In free-market conditions imports will compete with home production and will assuredly cause prices of home-killed beef to be lower than they would otherwise be. It is in the interest of all parties that an orderly system of marketing supplies be evolved.

Pattern of production and consumption in the exporting countries obviously affects the availability of imports on the British market. Subsequent papers will consider the problem of seasonality of overseas supplies. The problem for British producers is whether they should take advantage of the relatively cheaper period of production which leads to the autumnal glut or whether they should attempt to switch some production to those periods of the year when supplies are relatively short. The adoption of new technique in the winter feeding of beef cattle might very well aid the producer in an attempt to even out supplies. Consideration to this and to the possibility of the cold storage of home-killed beef will be given in a further paper.

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APPENDIX

Annual U.K. Beef and Veal Supplies (Carcass Meat) Pre-war and 1940–53

Year	*Home*[1] *production*	*Net Imports*[2]	*Total*	*% Home produced*	*% Imported*
		Thousands of tons			
Pre-war average	615·0	582·0	1,197·0	51·4	48·6
1940	581·9	528·6	1,110·5	52·4	47·6
1941	535·5	522·3	1,057·8	50·6	49·4
1942	475·8	462·9	938·7	50·7	49·3
1943	477·1	308·6	785·7	60·7	39·3
1944	517·1	339·7	856·8	60·4	39·6
1945	546·8	201·1	747·9	73·1	26·9
1946	569·8	405·8	975·6	58·4	41·6
1947	508·6	508·3	1016·9	50·0	50·0
1948	497·7	362·7	860·4	57·8	42·2
1949	527·3	362·3	889·6	59·3	40·7
1950	630·4	332·5	962·9	65·5	34·5
1951	645·6	157·0	802·8	80·4	19·6
1952	594·7	130·6	725·3	82·0	18·0
1953	609·9	307·9	917·8	66·5	33·5

[1] Includes production from fat animals imported from Eire.
[2] Includes fresh meat imported from Eire.

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RECOGNITION OF RYEGRASS SPECIES AND STRAINS IN THE SEEDLING STAGE[1]

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Summary

This paper describes studies on the early growth and seedling stages of species and strains of the genus *Lolium* with the following aims:

1. to find out to what extent the species and strains can be distinguished on the basis of seedling morphology;
2. to develop a method for seedling identification of the different species and strains.

Seeds were sown in boxes in the glass-house at different times of the year and various observations recorded on them.

It has been found possible to identify the different species and strains by a study of their seedling characters. A key has been prepared leading to the identification of the different species and strains in the seedling stage, grown under suitable conditions of light and temperature.

A classification of *Lolium* species into general types based on their seedling characters is consistent with that based on their adult characters.

COOPER and Saeed [1] have emphasized the importance of a study of the comparative morphology and physiology of related ecological forms within one species or between closely related species. The present paper is concerned with a comparative study of the morphology of the seedlings of the different species and strains of the genus *Lolium*. One object of this study was to develop a practical method of identification of the different species and strains in the seedling stage. The literature available on the subject shows that under proper conditions of temperature or light seedlings of different varieties manifest characteristic morphological differences.

Material and Methods

Species and strains studied.—Species of *Lolium*, which are all diploid with $2n = 14$, can be arranged in two groups: *The first group* comprises three outbreeding species, *L. rigidum* (Wimmera ryegrass), *L. italicum* (Italian ryegrass), and *L. perenne* (Perennial ryegrass). The range of ecological types within this group may be summarized thus: *Lolium rigidum* is an annual semi-erect plant with lax flowering stems. *L. italicum* is normally a biennial of a rather erect and tufted growth habit, though the stems carry more leaf than *L. rigidum*. Tillering is not so pronounced as in *L. perenne*. Four distinct types of *L. perenne* were studied, one commercial and three bred strains. All types are less erect in growth habit and more stemmy than the other two species. Aberystwyth S.24 is erect and early-flowering like Irish commercial but more

[1] These studies were carried out by the writer at the Welsh Plant Breeding Station, Aberystwyth, in the years 1946 and 1947 and the data were presented in part fulfilment of the requirements for the degree of M.Sc. of the University of Wales.

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leafy and persistent. Aberystwyth S.23 is late-flowering and high-tillering, and prostrate in habit. Aberystwyth S.101 is slightly earlier than S.23 and rather more erect [1].

The second group comprises four inbreeding species. They are all low-tillering, sparsely leafy annuals of little agronomic value. *L. loliaceum* is small and prostrate. *L. temulentum*, *L. arvense*, and *L. remotum* are larger and rather erect in habit.

Although the term 'strain' is commonly used only for the pedigree selected types, in this paper each of the above species or types is referred to as a 'strain' for purposes of convenience.

Methods.—Seeds were sown in boxes in the glass-house. It was statistically determined that two boxes per strain were enough to give the minimum variation in seedlings due to variation in boxes. Thirty observations at random, distributed over the two boxes, were found to be a reasonable minimum for taking observations on most of the seedling characters. However, germination and rate of leaf and tiller production were observed on all the seedlings present.

Observations recorded.—(i) Germination. (ii) Rate of leaf production: seedlings showing second and subsequent leaf stages were counted. Seedlings were regarded as being in the second-leaf stage when this leaf was just emerging from the fold of the first, and so on. (iii) Length and width of first, second, and third leaves on the same seedling at the fifth leaf stage. (iv) Tiller-bud production, rate of tillering and number of tillers at the fifth-leaf or later stage. (v) Degree of prostrateness: the angle made by the primary axis with the soil level, at the fifth-leaf stage.

Results

Germination.—The results for this character may be summarized as follows. Italian ryegrass was quick to germinate and maintained this lead until germination was completed. Wimmera, Irish, and S.24 followed Italian but did not differ significantly from each other. Wimmera was sometimes quicker to start than Irish and S.24 but took longer to complete as some seeds showed delayed germination. S.101 was generally slower than the above strains. S.23 was slow to germinate and also slow to finish. Of the remaining annual species, *L. remotum* was quicker to germinate than Wimmera and S.24. *L. temulentum* and *L. arvense* were somewhat slower. *L. loliaceum* was very slow to start, being the slowest of all the species, and also took longest to complete germination.

Rate of leaf production.—Table 1 shows the percentages of seedlings with the third leaf emerging, on different days after sowing. Wimmera was very fast in attaining the various growth stages and by the third-leaf stage it overtook and went ahead of all other strains except *L. remotum*.

Length and width of first and subsequent leaves.—Figs. 1 and 2 indicate the variations and average values in leaf-length and leaf-width of different strains for sowings made in April, May, and June. Table 2 gives the mean values of these characters for sowings in February and April. Characteristic differences are noted between the different strains.

Wimmera has short broad leaves and S.101 long narrow leaves. The

TABLE 1. *Percentage of Ryegrass Seedlings with (1) Third leaf emerging; (2) Tiller in Axil of Coleoptile; on various days after sowing*

First Series. Seed sown 11 February 1947:

Days after sowing		*32*	*33*	*34*	*35*	*36*	*37*	*38*	*39*	*41*	*42*	*43*	*44*	*45*
Italian .	(1)	2·1	3·2	7·4	63·2	80·0	96·8	97·9	100	..	..	..	..	..
(Bb 442)* .	(2)	0	3·2	7·4	14·7	27·4	36·8	54·7	60·0	64·2	66·3	..	..	..
Italian . .	(1)	1·3	5·3	18·7	74·7	84·0	92·0	96·0	98·0	100	..	..	..	..
(Bb 409) .	(2)	0	8·0	13·3	29·3	37·3	45·3	57·3	62·7	65·3	66·7	..	..	..
Wimmera .	(1)	0	1·7	7·3	46·3	75·7	89·3	96·6	98·8	98·8	98·8	99·4	99·4	100
(Ba 4944) .	(2)	0	5·1	15·8	49·3	64·9	75·1	80·5	83·3	83·3	83·9	84·4	84·4	85·0
Irish . .	(1)	0	0	0	4·6	19·5	47·1	79·3	91·9	98·8	98·8	100	..	..
(Ba 4953) .	(2)	0	0	0	0	2·3	8·9	9·2	13·8	17·2	18·4	19·5	19·5	19·5
Irish . .	(1)	0	0	0	0	0	4·8	28·6	50·8	92·0	95·2	96·8	96·8	100
(Ba 4443) .	(2)	0	0	0	0	1·6	4·8	11·1	19·0	30·2	34·9	36·5	38·1	38·1
S.23 . .	(1)	0	0	0	10·0	32·4	38·1	58·7	84·4	92·2	96·9	98·4	98·4	100
(LW/45) .	(2)	0	0	0	0	1·5	1·5	9·5	10·2	18·5	20·0	20·0	22·2	22·2
S.23 . .	(1)	0	0	0	0	0	4·1	14·9	39·2	77·0	90·5	95·9	98·6	100
(LW/45, 3rd and 4th cut)	(2)	0	0	0	0	0	0	0	4·0	7·8	9·1	9·1	9·1	9·1
S.24 . .	(1)	0·7	0·7	0·7	16·6	53·6	65·1	87·5	95·4	96·1	97·4	98·7	100	..
(BM/D) .	(2)	0	0	0	3·3	9·9	16·4	27·6	35·3	38·6	41·2	41·2	42·5	42·5
S.101 . .	(1)	0	0	0	1·1	11·1	20·0	50·5	83·5	96·7	97·8	98·8	98·8	100
(GH/44–45) .	(2)	0	0	0	0	1·1	3·3	3·3	10·9	14·1	15·2	15·2	16·3	..
S.101 . .	(1)	0	0	0	0	12·5	17·0	56·2	92·1	98·9	98·9	98·9	100	..
(BF/45) .	(2)	0	0	0	0	3·4	5·7	10·1	18·9	28·9	28·9	30·0	32·2	32·2

* Numbers in parentheses indicate the Welsh Plant Breeding Station Stock numbers.

Second Series. Seed sown on 15th April 1947:

Days after sowing		*14*	*15*	*16*	*17*	*18*	*20*	*21*	*22*	*23*	*24*	*25*	*26*	*27*
L. temulentum	(1)	0	0	0	38·1	42·8	81·4	100	..	..	..	..	..	..
	(2)	0	0	2·4	21·4	40·5	69·8	79·1	..	..	..	..	..	..
L. loliaceum .	(1)	0	0	0	0	0	0	7·9	52·4	80·9	88·6	96·8	96·8	96·8
	(2)	0	0	0	0	0	0	19·8	50·8	59·2	65·1	69·8	71·1	71·1
L. arvense .	(1)	0	0	0	1·0	2·0	40·0	74·0	94·0	98·0	98·0	100	..	..
	(2)	0	0	1·0	5·0	16·0	64·0	87·0	90·0	93·0	94·0	95·0	..	..
L. rigidum .	(1)	0	1·0	11·0	63·0	79·0	98·0	100	..	..	..	..	..	..
(Ba 5189) .	(2)	7·5	17·5	42·0	62·0	71·0	89·0	90	..	..	..	..	..	..
L. rigidum .	(1)	1·1	2·3	30·3	80·2	92·7	98·9	100	..	..	..	..	..	..
(Ba 4944) .	(2)	15·7	34·8	66·3	78·0	90·1	92·7	95·4	..	..	..	..	..	..
L. remotum .	(1)	0	0	69·6	91·3	95·7	100	..	..	..	..	..	..	..
	(2)	0	0	0	2·2	2·2	2·2	..	..	..	..	..	..	..
S.23 . .	(1)	0	0	0	0	10·8	64·9	83·8	97·3	100	..	..	..	..
(LW/45, 3rd and 4th cut)	(2)	0	0	0	5·5	10·8	37·8	43·2	45·9	45·9	..	..	..	..
S.24 . .	(1)	0	0	8·8	58·8	64·7	100	..	..	..	..	..	..	..
(BM/D) .	(2)	0	14·7	23·5	41·2	52·9	82·3	..	..	..	..	..	..	..

TABLE 2. *Mean Values of Various Ryegrass Seedling Characters*

First Series. Seed sown 11 February 1947:

Species or strain	Mean date of appearance of fifth leaf	Leaf length, cm.			Leaf width, cm.			Angle between main axis and ground level (degrees)		Number of Tillers		General Index	Third-leaf ratio width: length
		First leaf	Second leaf	Third leaf	First leaf	Second leaf	Third leaf	At 4th-leaf stage	At 5th-leaf stage	At 5th-leaf stage	On 14.4.47		
Italian (Bb 442)	29·23 ±0·319 (Mar.)	5·00 ±0·134	5·83 ±0·160	8·29 ±0·286	0·161 ±0·0042	0·281 ±0·0072	0·328 ±0·0071	78·3 ±1·642	69·3 ±2·447	4·00 ±0·216	22·57 ±0·924	1·459	0·039
„ (Bb 409)	28·53 ±0·311 (Mar.)	4·91 ±0·170	6·18 ±0·019	8·72 ±0·378	0·150 ±0·0047	0·280 ±0·0064	0·339 ±0·0069	..	68·7 ±2·929	3·73 ±0·188	24·30 ±1·178	1·487	0·039
Wimmera (Ba 4944)	29·77 ±0·586 (Mar.)	4·30 ±0·156	5·51 ±0·194	6·88 ±0·335	0·183 ±0·0038	0·305 ±0·0064	0·341 ±0·0074	60·0 ±3·462	46·7 ±3·799	3·77 ±0·186	25·03 ±1·402	1·251	0·049
Irish (Ba 4953)	32·90 ±0·366 (1st Apr.)	3·72 ±0·147	5·06 ±0·158	6·86 ±0·218	0·154 ±0·0053	0·268 ±0·0075	0·300 ±0·0055	72·3 ±1·870	58·3 ±2·872	2·53 ±0·155	12·23 ±0·561	1·206	0·044
„ (Ba 4443)	33·77 ±0·422 (2nd Apr.)	3·87 ±0·122	5·26 ±0·141	7·15 ±0·203	0·170 ±0·0038	0·283 ±0·0049	0·308 ±0·0054	67·7 ±2·191	48·0 ±3·104	3·50 ±0·175	13·83 ±0·664	1·222	0·043
S.23 (LW/45)	30·87 ±0·423 (Mar.)	3·31 ±0·078	3·88 ±0·084	5·17 ±0·133	0·153 ±0·0037	0·257 ±0·0056	0·291 ±0·0045	74·3 ±2·146	63·7 ±2·402	2·63 ±0·186	15·93 ±0·871	1·068	0·056
„ (LW/45, 3rd and 4th cuts)	33·50 ±0·439 (2nd Apr.)	3·14 ±0·098	3·63 ±0·087	4·89 ±0·146	0·148 ±0·0057	0·235 ±0·0061	0·265 ±0·0051	68·7 ±2·432	53·0 ±2·947	2·67 ±0·158	13·07 ±0·734	0·969	0·054
S.24 (BM/D)	32·23 ±0·210 (1st Apr.)	4·07 ±0·108	5·00 ±0·129	6·84 ±0·212	0·172 ±0·0041	0·278 ±0·0058	0·308 ±0·0039	79·3 ±1·826	67·3 ±2·403	3·63 ±0·191	15·47 ±0·792	1·292	0·045
S.101 (GH/44–45)	34·27 ±0·203 (3rd Apr.)	3·74 ±0·076	5·20 ±0·120	7·16 ±0·786	0·152 ±0·0039	0·258 ±0·0045	0·290 ±0·0045	75·0 ±1·129	65·0 ±1·985	2·83 ±0·134	11·67 ±0·583	1·265	0·041
„ (BF/45)	33·03 ±0·426 (2nd Apr.)	3·68 ±0·121	4·70 ±0·106	6·48 ±0·162	0·151 ±0·0047	0·255 ±0·0074	0·283 ±0·0046	77·7 ±1·211	68·0 ±2·179	3·17 ±0·183	14·00 ±0·679	1·228	0·043

Second Series. Seed sown 15 April 1947:

	[*May*]											
Wimmera (Ba 4944) .	8·90	5·52	6·99	8·33	0·178	0·300	0·347		19·83	5·87		0·042
	±0·422	±0·145	±0·136	±0·142	±0·0044	±0·0053	±0·0084		±3·276	±0·122		
,, (Ba 5189) .	9·60	5·00	6·76	8·11	0·176	0·297	0·349		25·33	5·70		0·043
	±0·304	±0·110	±0·199	±0·338	±0·0033	±0·0053	±0·0059		±3·729	±0·157		
L. temulentum . .	12·63	9·14	11·61	16·83	0·329	0·449	0·568		75·67	4·63		0·034
	±0·297	±0·187	±0·201	±0·359	±0·012	±0·0092	±0·0075		±2·138	±0·173		
L. arvense . .	14·57	8·23	10·69	15·06	0·325	0·433	0·563		68·67	5·70		0·037
	±0·232	±0·121	±0·127	±0·198	±0·0067	±0·0077	±0·0065		±1·979	±0·097		
L. remotum . .	9·60	7·31	9·26	12·65	0·273	0·326	0·454		79·33	3·63		0·036
	±0·261	±0·098	±0·113	±0·141	±0·0049	±0·0039	±0·0046		±1·248	±0·092		
L. loliaceum . .	16·33	5·62	7·52	11·13	0·214	0·336	0·373		34·67	5·60		0·034
	±0·211	±0·049	±0·171	±0·219	±0·0036	±0·0056	±0·0051		±2·041	±0·153		
S.24 (BM/D) . .	11·47	5·62	7·92	9·82	0·181	0·300	0·349		61·67	5·97		0·036
	±0·343	±0·122	±0·178	±0·260	±0·0041	±0·0055	±0·0058		±3·018	±0·221		
S.23 (LW/45, 3rd and 4th cuts)	14·43	4·55	6·20	8·29	0·151	0·270	0·306		42·33	5·23		0·037
	±0·340	±0·171	±0·171	±0·256	±0·0053	±0·0076	±0·0075		±3·454	±0·243		

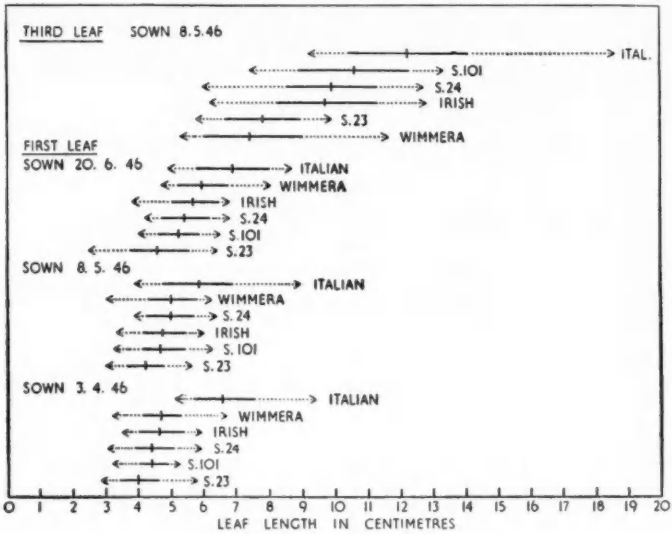
THIRD LEAF SOWN 8.5.46
ITAL.
S.101
S.24
IRISH
S.23
WIMMERA
FIRST LEAF
SOWN 20. 6. 46
ITALIAN
WIMMERA
IRISH
S.24
S.101
S.23
SOWN 8. 5. 46
ITALIAN
WIMMERA
S. 24
IRISH
S. 101
S. 23
SOWN 3. 4. 46
ITALIAN
WIMMERA
IRISH
S.24
S.101
S.23
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
LEAF LENGTH IN CENTIMETRES

FIG. 1

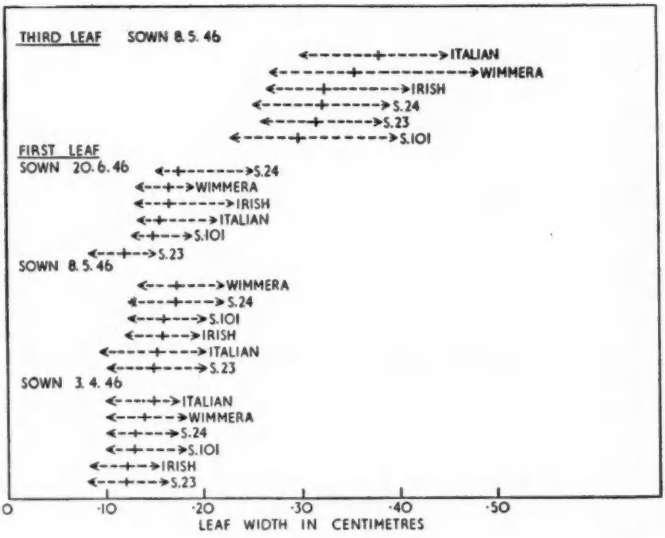
THIRD LEAF SOWN 8.5.46
ITALIAN
WIMMERA
IRISH
S.24
S.23
S.101
FIRST LEAF
SOWN 20.6.46
S.24
WIMMERA
IRISH
ITALIAN
S.101
S.23
SOWN 8.5.46
WIMMERA
S.24
S.101
IRISH
ITALIAN
S.23
SOWN 3.4.46
ITALIAN
WIMMERA
S.24
S.101
IRISH
S.23
0 ·10 ·20 ·30 ·40 ·50
LEAF WIDTH IN CENTIMETRES

FIG. 2

ratio width/length is a more useful diagnostic character than the absolute value for width.

Tiller-bud production, rate of tillering, and number of tillers.—In Table 1 are set out the values for these characters. Although a bud was always present in the axil of the coleoptile its rate of development into a tiller varied from strain to strain and was also influenced by environmental conditions. It is also apparent (Table 2) that some strains responded to favourable growing conditions better than others, and under such conditions, despite the initial disadvantage of a smaller percentage of seedlings producing the coleoptylar tiller, by the fifth-leaf stage they overtook and even surpassed the other strains.

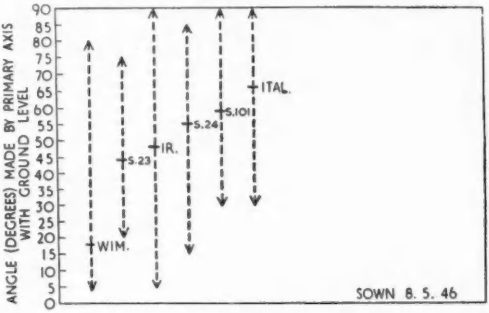

FIG. 3

In Table 2 are given the numbers of tillers 62 days after sowing, for the February-sown seedlings. Italian and Wimmera continued to tiller quickly until 14 April. Irish was quick in growth and tillering up to the fifth-leaf stage, but in a fortnight it began to lag behind the bred strains.

Degree of prostrateness.—In Fig. 3 are shown the variations and mean values of the angle made by the primary axis with the soil level, at the fifth leaf stage, for May 1946 sowing. Table 2 gives the mean values for these characters for seedlings sown in February and April 1947. Although variations are great and the ranges overlap, on the whole certain strains were more prostrate than others.

General index.—Anderson and Whitaker [2] have described a statistical method which combines two or more separate measurements into a single index. In the present study, a general index was calculated as follows:

General Index $= \sqrt{(A^2+B^2+C^2+D^2+E^2+F^2+G^2+H^2)}$, where

A - - - Mean length of first leaf in decimetres,
B - - - Mean length of second leaf in decimetres,
C - - - Mean length of third leaf in decimetres,
D - - - Mean width of first leaf in centimetres,
E - - - Mean width of second leaf in centimetres,
F - - - Mean width of third leaf in centimetres,
G - - - Mean number of tillers at fifth-leaf stage, divided by 10,
H - - - Mean angle made by primary axis at fifth-leaf stage, divided by 100.

This General Index might prove another useful means to differentiate between S.24 and Irish, since Irish invariably shows a lower value than any other *Lolium* strain.

Descriptive key.—It has been found possible to distinguish strains as early as the fifth-leaf stage. Although measurements and counts would be necessary in some cases, the different lots could be tentatively identified by observations alone. Indeed, no measurements may be necessary in identifying such strains as Wimmera, S.23, Italian, *L. temulentum*, *L. remotum*, and *L. loliaceum*.

For seedlings grown under good conditions of temperature and light, the following key is suggested for identification of the different strains:

I. Erect, very long leaves, successive leaves increasingly longer:

(A) A very small percentage of seedlings produce the tiller in the axil of the coleoptile; leaves only fairly long but wide relative to length . . . . . *L. remotum*

(B) A high percentage of seedlings produce the tiller in the axil of the coleoptile:

(1) Leaves very long and wide, ratio of width to length high *L. temulentum* or *L. arvense*

(2) Leaves only fairly long, ratio of width to length low *L. italicum*

II. Leaves only moderately long:

(A) Prostrate, successive leaves decreasingly long; leaves very wide relative to length; a very high percentage of seedlings produce the tiller in the axil of the coleoptile; very quick growth; diffused maroon pigmentation on leaf sheath *L. rigidum*

(B) (1) Delayed germination, successive leaves increasingly long, leaves very wide relative to length; somewhat prostrate; diffused purple pigmentation on leaf sheaths *L. loliaceum*

(2) Somewhat slow growth; successive leaves increasingly long, leaves narrow relative to length; only a small percentage of seedlings produce the coleoptylar tiller; erect; deep red pigmentation.

(*a*) Seedlings uniform, erect; relatively greater increase in length from second to third leaf compared with (*b*), and subsequent growth vigorous *L. perenne* (S.24)

(*b*) Seedlings not uniform; somewhat prostrate, subsequent growth not so vigorous *L. perenne* (Irish).

III. Leaves small; wide relative to length; initial growth somewhat slow; relatively small percentage of seedlings produce a coleoptylar tiller; somewhat prostrate; deep-red pigmentation *L. perenne* (S.23)

This key, supplemented with a table giving the average values for various characters of seedlings of different strains grown under comparable conditions, should lead to the identification of every strain. The order of magnitude of the terms 'very long', 'fairly long', 'moderately

long', as used in this key, may be seen from the measurements given in Table 2 and those plotted in Fig. 1.

By the use of this key for the identification of ten lots of different strains of origin unknown to the author, from seedlings sown in boxes, a satisfactorily high proportion of correct identifications was obtained.

Discussion

From the study of large populations of adult plants and their breeding behaviour Jenkin and Thomas [3] divided *Lolium* into the following six general types, or groups, sufficiently distinct to rank as independent species:

1. *L. perenne* L. (Non-annual; wind-pollinated).
2. *L. italicum* A.Br. (Non-annual; wind-pollinated).
3. *L. rigidum* Gaud. (Annual; wind-pollinated).
4. *L. loliaceum* Hand. Maz. (Annual; self-pollinated).
5. *L. remotum* Schrank. (Annual; self-pollinated).
6. *L. temulentum* L. (Annual; self-pollinated).

The author's seedling studies conform with the above classification.

L. perenne.—The seedlings of different strains of *L. perenne*, viz. Irish, S.24, S.101, and S.23, although varying between themselves, collectively differ from those of *L. italicum* and *L. temulentum* in the much smaller length of leaf and somewhat greater prostrateness; from *L. rigidum* in slower growth, narrower leaves, a tendency for the successive leaves to be increasingly long, more erect habit, and the nature of pigmentation. They seemed to approach *L. loliaceum* in the seedling characters but differed from it in quicker germination, smaller and much narrower leaves and the type of pigmentation.

L. italicum.—The seedlings differ from those of *L. perenne* in characters already discussed. From *L. rigidum* they differ in much longer leaves and far greater erectness, and from *L. loliaceum* in the same characters and a far quicker growth. They differ from *L. temulentum* and *L. arvense* in smaller and much narrower leaves and from *L. remotum* in longer but narrower leaves and in the possession of a far greater percentage of seedlings producing the tiller in the axil of the coleoptile.

L. rigidum.—The seedlings differ from those of *L. perenne* and *L. italicum* in characters discussed above. They differ from *L. temulentum*, *L. arvense*, and *L. remotum* in the same characters as from Italian, and from *L. remotum* further in having a far greater percentage of seedlings in which the coleoptylar bud grows into a tiller. They differ from *L. loliaceum* in the slower growth, much longer leaves, relatively greater increase in length in successive leaves and less prostrate habit of the latter.

L. loliaceum.—The seedlings differ from *L. perenne*, *L. italicum*, and *L. rigidum* in the characters described above. From *L. remotum* and *L. temulentum* types they differ in their slow germination, far smaller leaves, and more prostrate habit.

L. remotum.—The seedling differences from the above four types have been considered. From *L. temulentum* type they differ in quicker germination, significantly smaller leaves, and in the fact that only a very

small percentage of seedlings produced the tiller in the axil of the coleoptile.

L. temulentum and *L. arvense*.—There was nothing to distinguish their seedlings, thus justifying their inclusion in one type.

The classification based on adult morphology is thus entirely consistent with that based on seedling characters. The justification of treating *L. loliaceum* and *L. rigidum* as distinct species and of including under one type *L. temulentum* and *L. arvense* is brought out. Similarly, no differences were noted between *L. italicum* and *L. westerwoldicum* seedlings in the above-mentioned test of the efficacy of the descriptive key, in which the latter was identified as Italian type, thus supporting its inclusion under the type *L. italicum*.

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THE USE OF FLEECE MEASUREMENT IN THE IMPROVEMENT OF MERINO FLOCKS IN QUEENSLAND

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Summary

The object of the investigations reported in this paper was to examine the accuracy of visual appraisal of Merino sheep in Queensland, and to ascertain how much improvement in the amount of genetic gain could be achieved by the use of quantitative measurements of fleeces instead of, or as an adjunct to, visual appraisal.

Background information on the use of fleece measurement is tabulated, and the way it is fitted into the management of stud Merino flocks in Queensland is described.

The results have shown that the use of fleece measurement as an aid in the selection of stud Merino sheep can greatly increase selection differentials for the characters that influence the quantity and quality of wool produced by Merinos in Queensland. The majority of these characters are highly heritable and the structure of the Merino Sheep Industry in Queensland should favour the transmission of genetic improvement wrought in the studs of the majority of the sheep that constitute Queenslands flocks.

OFFICIAL statistics show that the average cut of wool per head of sheep in Queensland has increased considerably since the Australian Merino was first recognized as a breed [1]. Several factors have probably contributed to these increases. Grazing lands have been developed; fencing and increased water facilities in the semi-arid pastoral country have allowed better utilization of the natural pastures. Better methods are available for the control of parasites and there are now remedies for nutritional diseases likely to decrease wool production. Grazing pressures have been reduced by the control of rabbits. In some small areas direct breed substitution, such as Corriedales or crossbreds for Merinos, has occurred. Changes of this type have taken place in the more favoured environments, relegating the Merino to the drier and usually less favoured areas.

The weights of many of the early clips were probably recorded as washed wool. Therefore, cuts per head of sheep in the last century may not be strictly comparable with those recorded today.

No doubt some of the increase in the cut per head that has occurred has been due to genetic improvement. However, the selection of Merinos has been almost entirely phenotypic and by visual appraisal. Most of this work is done by professional sheep classers who are employed to 'cull' ewes as well as to select rams. As most of the characters contributing to clean wool weights are highly heritable, the amount of genetic gain depends upon the intensity of selection and *the accuracy with which the characters can be assessed by visual appraisal.*

[1] Director of Sheep Husbandry. [2] Senior Husbandry Officer.

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The object of the investigations reported in this paper was to examine the accuracy of such assessment by visual appraisal alone, and to ascertain how much improvement in the amount of genetic gain could be achieved by the use of quantitative measurements of fleeces instead of or as an adjunct to visual appraisal.

A fleece-measurement laboratory capable of handling 10,000 wool samples a year was established at Brisbane within the Sheep and Wool Branch of the Queensland Department of Agriculture and Stock in 1949. It operates as a public facility and is equipped to determine clean scoured yield, burr, residue and moisture content, staple length, crimps per inch, fibre diameter, standard deviation and coefficient of variation in fibre diameters, fibre populations, and S/P ratios.[1] The application of fleece measurement to sheep breeding in Queensland arose partly out of data compiled by the C.S.I.R.O. Division of Animal Health and Production.

The methods used in the fleece-measurement laboratory are basically those described by Bosman and van Wyk [2], Carter [3], Lipson [4], A.S.T.M. on Textile Materials [5], Land, and Roberts (private communications) and C.S.I.R.O. [6].

The results obtained by the use of fleece measurements made in this laboratory have shown that selection of stud sheep in Queensland by fleece measurement can result in an improvement in quantity and quality of wool about twice as great as that obtainable by visual appraisal alone.

Since the establishment of the laboratory, extension workers in the Sheep and Wool Branch have brought the advantage of fleece measurement to the notice of woolgrowers in Queensland. Many are now using the available facilities and some have incorporated fleece measurement in their selection programmes.

The Structure of the Queensland Merino Sheep Industry

Queensland's flock is composed almost entirely of Merinos. Since 1890 it has averaged 18½ million, although the State's sheep population has varied widely during the last sixty years. These sheep, which are referred to as flock sheep, are distributed amongst some 4,600 properties. Four thousand of these carry breeding flocks, the rams for which are bought from studs.

There are seventy-four Merino studs in Queensland. One has been established ninety-nine years; some for as few as six years. Until recently no stud was closed to the introduction of outside blood; most have drawn leading sires from studs in New South Wales or from one another. Thirty-four studs mate, on an average, more than 1,000 ewes per annum. Seven of these have introduced rams from another stud during the past twelve years, and thirteen from two other studs. The remaining fourteen introduced rams from three or more other studs (Australian Merino Stud Flock Register).

The Merino Studs located in Queensland are now supplying about 75 per cent. of all the rams required for mating with the State's ewe

[1] Ratios of secondary to primary follicles [7].

flocks. Therefore, a large proportion of the genetic improvement wrought in them should be transmitted finally to the flocks that buy their rams. The laboratory's services are being used extensively by over half of the studmasters in the State.

In seeking the field application of fleece measurement a number of factors had to be considered.

Input/Output Relationships of Fleece Measurement in Flock Improvement

A number of characters contribute to fleece weight; the available selection pressure has to be divided among them. Therefore, in setting up plans to incorporate fleece measurement in programmes for the improvement of stud sheep, the importance of the following factors emerged:

(1) The contribution made by different animals to genetic improvement.
(2) The economic importance of the characters to be measured.
(3) The amount of variation within the flock for each character.
(4) The extent to which measurements increase the accuracy of selection for each character.
(5) The immediate return resulting from measuring fleece characters. This will depend upon a combination of factors 1, 2, and 3.
(6) The long-term genetic gain resulting from using measurement as an aid to selection. This will depend upon factors 2 and 3 and the heritability of the respective characters being measured.
(7) The relationship between the work involved in measuring fleece characters and the immediate economic returns or the long-term genetic gains resulting from fleece measurement.

Because of the greater intensity of selection that can be adopted, and because of the greater number of offspring they beget, rams make by far the greatest contribution to genetic progress. Morley (private communication) estimates that 45 per cent. of the total improvement comes from the selection of rams to breed rams. The selection of rams to breed ewes contributes a further 30–40 per cent. of the total improvement. Ram selection can therefore contribute 80 per cent. of the genetic improvement possible in a Merino breeding plan.

As Queensland's flock is comprised mainly of Merinos, a very large proportion of the clip is classed as being of a 64s count.[1] In 1952–3, for instance, only 6·4 per cent. of the clip was classified as 70s or finer count and only 9·2 per cent. as 60s or coarser. The remainder was classed as 64s/66s. There is a negative correlation between fine fibre diameter and high fleece weight and there are not very large differences between the prices commanded by medium and fine Merino wools offered for sale in Queensland. Therefore, high fleece weight emerges as the character of greatest economic importance.

[1] The trade count is the number of hanks, each 560 yards long, that can be spun from one pound of combed tops made from the wool in question [8, 9].

Thirty studmasters and sheep-classers, who attended a school for members of the Queensland Merino Stud-Sheep Breeders' Association

TABLE 1. *Classing Results—Thirty Sheep Classed by Thirty-one Studmasters and Sheep-classers**

Sheep number	*Votes received*	*Greasy fleece wt. in lb.*	*Clean fleece wt. in lb.*	*Value in pence per lb. clean wool*	*Total Value of Fleece in pence*
6	25	6·94	4·03†	197	793
1	23	6·69	3·58	193	691
9	19	7·12†	3·99	200	799†
4	19	7·12†	3·92	204†	800†
10	16	7·81†	4·19†	204†	854†
28	13	6·00	3·21	213†	684
17	11	7·88†	4·17†	202†	842†
26	7	6·25	3·27	195	637
8	4	6·88	3·82	204†	779
5	4	7·00	3·50	200	700
23	3	7·12†	3·62	195	707
19	2	8·19†	4·43†	188	833†
27	2	6·50	3·53	195	688
20	2	6·88	3·63	176	638
16	1	7·56†	4·19†	187	783
29	1	6·94	3·66	187	684
14	1	6·31	3·41	195	666
21	1	5·81	2·99	200	597
11	1	5·75	3·02	187	565
7	0	6·56	3·65	200	729
15	0	6·75	3·59	193	693
2	0	6·75	3·22	193	621
25	0	6·44	3·48	177	617
30	0	6·25	3·12	182	568
18	0	6·88	3·78	188	711
13	0	7·50	3·52	188	663
12	0	5·75	3·09	200	619
3	0	6·19	3·35	184	617
24	0	6·19	2·88	204†	587
22	0	5·56	2·89	193	557

* In this table sheep are ranked in order of popularity (votes received). The weight and value of each fleece are also given. The current market prices per lb. of wools of the different manufacturers' types were obtained from the Brisbane Wool-Selling Brokers' Association after the fleeces had been placed in their ARWC types by the brokers' experts.

† Signifies the best sheep in the group for the character concerned. The best five sheep in order of commercial return were Nos. 10, 17, 19, 4, 9.

held at Tambo in Central Queensland during September 1954, were asked to select, by visual appraisal alone, the best five sheep on commercial return and to 'cull' the worst 33 per cent. from a flock of young ewes. A positive selection differential of 0·25 lb. of greasy wool was obtained from the culling of 33 per cent. of the sheep. The five sheep chosen by popular acclaim as being the best gave a positive selection

differential of 0·42 lb. of greasy wool. When the measurement of fleece weight was combined with a visual assessment of the animals, a positive selection differential of over 1·0 lb. of greasy wool was obtained.

Table 1 shows how the sheep were ranked in order of popularity by those participating in the trial.

Similar data are on record for over 100 studmasters, sheep-classers, and woolgrowers who have attended extension schools at which the use of fleece measurement has been explained and demonstrated.

The efficiency of selection by visual appraisal varied considerably. At its best it had a degree of accuracy comparable with that from selection on greasy fleece weight. In no instance was great accuracy shown when selection was for either clean fleece weight or commercial return. The result of selection on clean-fleece weight closely approximates that from selection on commercial return.

In the light of our present knowledge, the heritabilities of the more important fleece characters are accepted as falling within the following ranges:

Character	*Heritability*
Greasy-fleece weight	30–40 (Rasmussen [10], McMahon [11], Terrill and Hazel [12], Rea [13], Morley [14].)
Clean-scoured weight	30–40 (Morley [14]).
Staple length	30–50 (Terrill and Hazel [12], Hazel and Terrill [15], Rae [13], Morley [14]).
Fibre diameter	35–50 (Turner and Kennedy (private communication.)
Quality number	20–40 (Morley [14]).
Fibre populations per unit area	10–60 (Turner and Kennedy (private communication).

It seems likely, therefore, that given reasonable selection pressure and accurate methods of selection, fairly rapid genetic progress might be made by mass selection for these characters.

The approximate amount of labour that may be required to measure the different characters of the fleeces shorn from 1,000 sheep is set out in Appendix No. 1.

Fleece Measurement in the Breeding of Stud Sheep

It was realized that any suggestion that a radical departure should be made from methods of visual appraisal, in which some people are considered to be skilled, to a greater dependence upon measurements, performed in distinct laboratories, would not necessarily be welcomed. Carefully planned extension work was necessary to overcome existing objections. The present organization of the sheep industry makes it difficult to reduce generation length along the ram-to-ram and ram-to-ewe paths; low reproduction rates make it difficult to reduce it on the ewe-to-ram and ewe-to-ewe paths. They also reduce the intensity of selection. Therefore, the higher selection differentials resulting from more accurate methods of selection are one of the important keys to increased genetic progress.

Fleece measurement is being incorporated in programmes for the

improvement of stud flocks in different ways. The particular requirements of different studs influence the way in which fleece measurements are used. But consideration is always given to the progress likely to result from the additional labour involved in fleece measurement.

Obviously, the best results will be obtained by concentrating upon the rams used as leading sires in closed studs. Rams are usually classed on phenotype when they are 16 to 18 months of age. About four or five times the number required as replacements for the leading sires are chosen and allowed to grow for another year or so before a final selection is made. These sheep are referred to as 'reserves' and usually comprise about 10 per cent. of the total number of rams available at classing.

When the rams are classed into the reserve grade particular attention is given to conformation and to wool characters which are assessed visually. Woolgrowers using fleece measurement as an aid in their final selection are encouraged to write a detailed description of the type of sheep they wish to breed and to list disqualifying faults. In deciding upon these, the probable heritability as well as any correlation between characters and the economic importance of the various faults have to be considered.

Appendix No. 2 summarizes the common faults against which selection is practised and indicates their significance.

The rams are ranked in descending order according to their clean-fleece weight. The staple length and fibre diameter of the sub-samples from the rams with the highest clean-fleece weights are then measured. The heaviest cutting rams falling within the stated tolerances of trade type and fibre diameter and having the greatest staple lengths are tabulated.

If there is anything to suggest that the sheep have low fibre populations or low S/P ratios these characters are determined from histological examination of skin samples. However, as the examination of skin sections for fibre population or S/P ratio is time-consuming, this work is not carried out unless there are special reasons to warrant it. Fibre populations are of little use unless skin area is also known.

Fairly accurate selection differentials can be obtained by weighing the fleeces from 25 per cent. of the rams remaining after the reserves have been selected. The sheep whose fleeces are weighed are chosen at random from all the rams in the same age group, including the culls.

In the final selection before mating greatest attention can be paid to wool characters. Selection at this time places greater emphasis on desired characters, as sheep with undesirable characters are mainly eliminated during the first classing.

The wool characters on which selection is based are summarized in Appendix No. 3, which also indicates their importance.

After classing, the reserve rams are shorn and sampled. The sheep are tagged or individually identified before shearing. A light raddle mark placed in the middle of the right hand side (i.e. whipping side) before shearing identifies the sampling area when the fleece is thrown out on the table, and facilitates sampling.

The fleeces are weighed immediately after they are shorn. When the fleece is thrown on the wool-classer's table the marked mid-side sample is taken from it and placed in an airtight tin with a card showing tag number of the sheep, weight of belly wool, and fleece weight.

On arrival at the laboratory these samples are classified for trade type and they are sub-sampled for the measurement of staple length, fibre diameter, and crimping.

When the flock of reserve rams is brought up for final classing at about 30 months of age the best 20 to 25 per cent. may have to be selected as top sires. This would represent about 2–3 per cent. of all the rams offered for initial classing at 18 months of age. At the final classing selection is made for the desired characters.

The classer has the sheep presented to him with a record of their performance at 18 months of age. An example of the way the results are presented is shown in Table 2. The classer looks for the sheep whose *type* he has outlined, cutting a *heavy fleece* in a specified *quality range*. If the best 20 or 25 per cent. on clean-wool weight conform to type and carry wool within the stated tolerances for quality, they are chosen. Whilst fibre diameter is a useful measurement for ranking sheep in order of fineness, it is not ideal for placing individual sheep in a quality range.

There are several scales, such as the 'Duerden', correlating fibre fineness with quality. Whilst these may be generally acceptable, it is doubtful if they can be applied when considering individual sheep. Fibre diameter can be markedly influenced by nutrition. Perhaps a better method would be to take the average fibre diameter of the rams measured as that which is acceptable. Individuals showing a marked deviation from this mean should be looked at carefully.

However, at the final classing the classer has a second opportunity of checking the quality of individual sheep. The sheep that are finally selected are the heaviest cutters that fall within the tolerances for wool quality and staple length and that show no signs of kemp when examined at the second classing.

This method of selection is still not ideal in that generation lengths are long and the selection differential is smaller than when selecting on fleece weight alone. However, studs have already accepted the use of fleece measurement in this form as it fits so easily into their standard sheep-breeding practices.

Ewe Selection.—Similar procedures are followed in selecting ewes to form or to replace those in the ewe nucleus. Care is taken to make the selection within age-groups. The ewes finally selected for the nucleus comprise the best of each age-group on visual appraisal and fleece measurement. However, because of the comparatively short length of the useful breeding life of ewes, young sheep are favoured for selection into a nucleus.

When the selection is to be made from maiden ewes the flock is classed by visual appraisal before shearing. At shearing time the fleeces are weighed and final selection is made on either greasy or clean-scoured fleece weight. However, as there is a correlation of +0·8 between greasy

TABLE 2. *Basis for the Final Selection of Four Leading Sires from Forty Reserve Rams*

The rams were arranged in descending order of clean-scoured fleece weight and the rams with ear tag numbers 215, 87, 109, 315 were finally selected. Three other rams were also selected for a second stud on another property. Only the results for the fourteen rams cutting the highest clean-scoured fleece weights are included. The + and − signs indicate the directions of the individual sheep from the flock average shown above

	Clean scoured fleece wt. (lb.)	*Greasy fleece wt. (lb.)*	*% Yield on dry wool basis*	*Staple length (in.)*	*Average fibre thickness (microns)*	*Coefficient of variation (%)*	*Visual quality number*	*Allocation of rams*
Flock average reserve rams only .	8·6	14·0	61·3	4	19·9	19·4	..	..
Sheep No.								
215 .	+2·2	+3·3	+0·9	0	+2·5	−1·4	64	1st
87 .	+2·1	+2·1	+5·2	0	+0·2	+0·5	64	1st
109 .	+2·1	+1·2	+0·1	+¼	−1·7	+0·9	64	1st
124 .	+2·0	+3·2	+0·1	−½	−0·1	+5·2	64	2nd (too short in staple) (too variable)
256 .	+2·0	+2·7	+1·7	−¼	+0·2	−0·5	64	Cull (black spot)
93 .	+1·8	+2·8	+0·4	0	−0·8	+5·7	58	Missing
315 .	+1·7	+3·1	−1·0	−¼	+1·4	+6·7	58	2nd (too variable)
133 .	+1·7	+3·0	−1·0	0	−0·6	−1·7	64	1st
288 .	+1·7	+1·7	+3·8	+¾	+1·4	+5·2	64	Reserve (little variable)
197 .	+1·6	+2·4	+0·7	+¼	−0·8	−0·8	64	Cull (Epididymitis)
264 .	+1·6	+2·6	−0·1	+¼	+0·5	+5·9	60	Reserve (Variable)
86 .	+1·5	+1·3	+4·5	+½	−1·2	−1·0	64	2nd
259 .	+1·5	+2·3	+0·4	+¾	+0·6	−0·6	60	2nd
376 .	+1·5	+2·6	−0·6	+½	−1·2	+0·4	66	2nd

and clean-scoured weights of samples submitted to the Wool Laboratory (unpublished data), the former is usually accepted as a useful guide.

Selection differentials can be calculated by weighing the fleeces of the sheep culled in the initial classing.

In some studs the final selection is made after the ewes had an opportunity to rear their first lambs. The flock is classed in the usual manner and maiden fleece weights are recorded. The ewes are mated and the final selection is made from those that rear a lamb from their first mating.

TABLE 3. *Results from Selecting Fifteen from a Flock of 511 Rams*

	Greasy fleece wt. (lb.)	*Clean-scoured wool wt. (lb.)*	*Staple length (in.)*	*Fibre diameter*
Unclassed ram flock .	14·3	8·4	..	..
All 367 rams . .	14·3	8·4	..	..
53 chosen by classer .	14·0	8·3	3·6	22 μ (60–64s)
15 finally selected . .	14·8	8·9	3·8	20·8 μ (64s)
Best 15 for each character	15·2	9·2	4·1	21·5 μ (64s)

Selection Differentials:

	Greasy fleece wt. (lb.)	*Clean scoured wt. (lb.)*
For initial culling of 144 (average of 367 kept, minus average of unclassed flock)	0·0	..
For classer's choice of 53 (average of 53 chosen by classer, minus average of unclassed flock) . .	−0·3	−0·1
For 15 finally chosen on measurement . . .	+0·5	+0·5
For best 15 on single characters	+0·9	+0·8

The Results of using Fleece Measurement in Improving Merino Flocks in Queensland

The selection differentials obtained by using fleece measurement in this way are far greater than those obtained by visual appraisal. As an illustration of results that can be achieved some figures pertaining to one stud are set out below.

There were 511 'two-tooth' rams and 144 were rejected in the initial classing of the stud. The classer culled a further 314 from the remaining 367—leaving 53, from which to choose a final 15. Wool samples were taken from each fleece after it had been weighed. Percentage yield, clean-scoured fleece weight, staple length, and fibre diameter were measured.

The results are presented in Table 3. The required fifteen rams were chosen on measurement after consideration of four characters—greasy wool weight, clean-scoured wool, staple length, fibre diameter.

A study of the distribution of each of the various characters around its average showed that this classing by visual appraisal only gave:

1. Some effective culling of sheep with very fine wools.
2. Effective culling of sheep with short-stapled fleeces.

A nucleus of 320 four-tooth ewes was also selected from a flock of 1,120. In making this selection fleece measurement was combined with visual appraisal. Accepting a heritability of 30 per cent. for clean fleece weight, the likely genetic gain in clean-wool weight from the two methods of selection is 0·045 lb. clean-scoured wool per sheep generation on the classer's choice and 0·105 lb. of clean-scoured wool per sheep generation by using visual appraisal for culling plus measurement for final selection. Comparable increases in the rate of genetic gain have been demonstrated in all the other studs using fleece measurement.

The cut per head of sheep in Queensland is said to have increased by about 2·25 lb. of greasy wool during the last fifty years. It is clear that extremely small selection differentials are likely to be obtained from visual appraisal of sheep. Probably about ten sheep generations have passed through the hands of Queensland studmasters during the last fifty years. It seems probable, therefore, that in the past the greater part of the increased cut per head has come from better land utilization rather than from genetic improvement.

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It is also desired to record our appreciation of the co-operation afforded by the studmasters which facilitated the application of fleece measurement, and that of the Queensland Merino Sheep-Breeders' Association which organized a school to acquaint its members with the principles and application of fleece measurement.

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Appendices overleaf

APPENDIXES

APPENDIX NO. 1. *Number of Man Hours Required to Measure the Various Characters in 1,000 Fleece Samples*

	Man hours	*Totals*
In the shearing shed:		
Weighing greasy fleeces, recording weights, and identifying sheep	40	..
Tabulating data obtained from weighing fleeces, calculating means, and selection differential	30	70
Sampling shorn fleece for laboratory examination	40	40
In the laboratory:		
Weighing samples, classifying for trade type, subsampling	160	..
Scouring	120	..
Weighing scoured wool, estimating burr, residue, and moisture contents	160	..
Calculation of clean-scoured yields and clean-fleece weights	50	490
Measuring staple length	80	80
Fibre diameter:		
Counting crimps per inch	120	..
Measuring fibre diameter, calculating coefficient of variation, tabulating results	2,880	3,000
Fibre populations and S/P ratios:		
Taking skin samples	80	..
Embedding, cutting, staining, examining sections, tabulating results, &c.	7,220	7,300

APPENDIX NO. 2. *The Characters against which Selection is Practised*

Character	*Economic importance*	*Probable heritability*	*Correlation*
Wool-blindness	Wool-blind sheep may be smaller and produce fewer lambs. (Terrill, [16]	High	
Undershot jaw	Interferes with sheep's ability to graze.	High (Kelley [17])	
Crooked legs Turkey hocks	Interferes with sheep's ability to walk. Predisposes to fly strike. (Seddon, *et al.* [18])	No published results known.	
Small body size	Small body size means small skin area and lowered sale value. (Lines and Peirce [19])		1. Number of fibres per unit area has slight negative phenotypic correlation with body size. 2. Body size and staple length have slight positive phenotypic correlation.
Excessive skin folds	1. Wrinkly sheep hard to shear. 2. Wrinkly sheep may have uneven fleeces. 3. Wrinkly sheep susceptible to blowfly strike (Seddon *et al.* [18])	High (Morley [14])	1. Strong negative correlation phenotypically between wrinkling and staple length; negative genetic correlation. 2. Strong negative correlation phenotypically between wrinkling and body size; probably negative genetic correlation.
Unevenness of wool cover especially on back	1. Influences wool-cut per head. 2. Allows fleece damage from sun's rays in tropics. 3. Influences price per pound.	No published results known.	
Harsh handle of wool	Influences price per pound.	No published results known.	Apparent correlation between handle and fibre diameter within a quality number.
Trade count beyond tolerances laid down	Influences price per pound.	Medium to high.	1. Requirements dictated by district and ewe flock. 2. Phenotypic correlation between trade count and fibre diameter.
Discoloured wool	1. Colour of wool influences price per pound. 2. Black or brown fibres decrease price per pound. 3. Sheep with black spots may sire black lambs (Kelley [20]) 4. Sheep with brown spots lower sale value.	High	
Short staple length	1. Influences fleece weight and price per pound. 2. May influence preservation of tip.	High	1. Slight positive phenotypic correlation between staple length and fibre diameter. Probably positive genetic correlation too. 2. Slight positive phenotypic correlation between staple length and body size—intermediate genetic correlation.
Kemp, especially on breech	Influences price per pound.	High	

APPENDIX NO. 3. *The Characters for which Selection is Practised*

Character	*Significance*	*Probable heritability*	*Assessment*	*Comments*
Live weight. Highest live weight compatible with the demands of the environment.	1. Large skin area correlated with high body weight. 2. Better resale value for heavy sheep.	High	1. Weigh sheep. 2. Estimate on appearance.	Consider live weight in relation to age, previous history and size, i.e. are the sheep well grown and heavy or small but fat?
Distribution of Wool. Should extend over whole of body and to the points, leaving the face open.	1. High utilization of available wool growing area. 2. Immediate sale value.	No published results known.	Visual appraisal.	
Evenness of Cover. Whole fleece should be even in staple length and trade count.	1. Influences cut per head. 2. Influences price per pound.	No published results known.	1. Visual appraisal. 2. Measure staple length on skin at different locations.	Special attention should be paid to the covering of the back.
Handle of Wool. Should be soft, but full and with ample body.	Influences price per pound.	No published results known. Probably high.	Manual appraisal.	Apparent correlation between handle and fibre diameter within a quality number.
Tip. Should be compact and blocky with little waste and/or penetration by dust.	Influences price per pound.	No published results known.	Visual appraisal.	Extremely important in some environments, especially the tropics.
Colour. Wool should be bright, soft creamy to off-white in colour. Fleece must be free of black; large brown or black spots on face and lower legs not tolerated.	Colour of wool influences price per pound.	High.	Visual appraisal.	
Staple length. Should be as long as possible, but compatible with trade counts and environmental conditions.	1. Influences weights, cuts and price per pound. 2. May influence preservation of tip.	High.	1. Visual appraisal. 2. Measure staples from mid-side.	1. Visual appraisal reasonably accurate. 2. Slight phenotypic correlation between staple length and fibre diameter. Probably positive correlation too. 3. Slight positive phenotypic correlation between staple length and body size—intermediate genetic correlation.
Greasy-fleece weight. Should be highest amongst all acceptable rams	Governs commercial re-	High.	1. Weigh.	Subject to considerable error.

Greasy-fleece weight. Should be highest amongst all acceptable rams.	Governs commercial return.	High.	1. Weigh. 2. Visual appraisal.	Subject to considerable error.
Clean-scoured fleece weight. Should be highest amongst all acceptable rams.	Governs commercial return.	High.	1. Weigh greasy fleece and scour mid-side sample. 2. Estimate on greasy fleece weight.	Correlation of +0·8 between clean scoured wool and greasy fleece weight in samples so far handled by the Wool Laboratory.
Yield. High yield probably desirable.	1. Governs commercial return. 2. May influence preservation of tip.	High.	1. Scour mid-side sample. 2. Visual appraisal.	
Fibre diameter (*measured*). Should be within tolerances required for diameter and evenness.	Influences cut per head.	High.	By microscopy.	1. Time consuming. 2. Correlated with staple length (see staple length).
Measured fibre populations. Should be as high as possible considering total skin area.	1. Influences cut per head. 2. May influence preservation of tip.	No published results known.	1. By cast method (Wilson [21]).	1. Number of fibres per unit area and fibre diameter very strong, negative correlation phenotypically, probably negative correlation genetically. 2. Number of fibres per unit area correlated with body size (see body size).
			2. By histological examination (Carter [3]).	About twice as time consuming as cast method.
S/P ratios. High ratio of secondaries to primaries, low percentage of primary follicles.	Influences occurrence of dogginess in wool, kemp, &c.	High.	1. By histological examination. 2. By observing hairiness of birth coats.	Very time consuming.

THE NUTRITIVE VALUE OF EAST AFRICAN HAY

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Summary

1. Data are presented on the composition, digestibility, and feeding value of ten grass hays, produced in the Central Province of Tanganyika (annual rainfall 20–23 inches).

2. The crude-protein contents of the dry matter varied from 3·7 to 9·2 per cent. and the crude-fibre figures ranged from 32·5 to 43·5 per cent. In the hays from the more mature herbage, the digestibility of the crude-fibre fraction exceeded that of the nitrogen-free extractives.

3. The more stemmy and less leafy *Chloris gayana* and *Andropogon caricosus* hays were considerably inferior to the other species in digestible crude protein and starch equivalent. The starch-equivalent values of the other species (31·7 to 39·8 per cent.) were similar to the energy values of medium–good quality United Kingdom hays but the contents of digestible crude protein (3·2 to 5·7 per cent.) were generally slightly lower. *Cynodon plectostachyum* first-cut hay contained the highest percentage of digestible crude protein but the aftermath hay of this species had a starch-equivalent value of only 31·7 per cent. The feeding values of the immature local *Panicum maximum* and *Pennesetum purpureum* hays and the hay from the exotic *Digitaria pentzii* were very similar, and intermediate between that of the first-cut *C. plectostachyum* and the two types of *Cenchrus ciliaris*.

SINCE the 17 million African-owned cattle in the East African territories secure the bulk of their nutrients from the consumption of grasses, information on the nutritive values of this important source of fodder is urgently needed. Unfortunately, there is such a multitude of grass genera, often with many species and varieties in each, that it would be impossible to investigate all without a large team of workers, and the limited number of hays studied in the present investigation omits many of fundamental economic importance. They were chosen because they were all grown at 3,500 ft. in the same season and alongside the green grasses previously reported upon from the Central Tanganyika plateau [1]. Climatic variations between seasons in the same locality and between different localities in the same season inevitably cause differences in the nutritive values of any given grass, while the variance is likewise augmented by differences in the stage of maturity. Species variance due to differences in maturity could be expected to be less for the feeding value of hays of comparable height and stemminess cut and cured at a similar stage of maturity, but weather conditions during curing can introduce a further set of variations. Mismanagement and unnecessarily rough handling during curing can also cause considerable losses of the more nutritive and tender leaves. All the grasses studied in these investigations were therefore handled with the same implements and care and it was fortunate that they were cured without being wetted by rain. It is not claimed that the hays were ideally prepared, but they probably represent the average quality which could be produced in

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practice in the particular season and environment in which they were grown.

Owing to the seasonal distribution of the limited rainfall in arid and semi-arid areas, the period of growth is restricted, but the rates of growth and maturation may be accelerated. The severity in restriction of herbage growth will naturally vary between seasons and districts, while the leaf:stem ratio, and the comparative vegetative growth of each, will show considerable diversity between genera and species. These changes can be expected to be most marked when the herbage remains ungrazed or uncut and are consequently very obvious in the naturally cured hays left uncut *in situ* in many of the African areas. The need for making hay from the different local species at the correct stages of maturity requires no emphasis because not only will losses in nutritive value, due to more advanced maturation, then be reduced but there will also be less wastage than that currently caused by the trampling and fouling of the cured, standing herbage during its collection and consumption by livestock. The limitations imposed by local climatic conditions may appreciably influence the chances of successful haymaking when the grasses are at their optimal stage of maturity, but much can be done to overcome this by regulating the time at which a field is closed to grazing. The grazing of the early flush of grass can be of great help in influencing the subsequent growth and maturity of herbage by the time the climatic conditions are suitable for haymaking, and consequently in postponing the development of the optimal stage of growth until the risks of rain-damage and curing delays are relatively small or even completely avoided. Stage of maturity is certainly of greater importance locally than the mere age of the crop, in determining nutritive values, as has been proved in many studies in other parts of the world. The figures in Table 1 illustrate the type of

TABLE 1. *Composition and Nutritive Value of Hays Made at Different Times of the Year*

(*Dry-matter basis*)

	First cut	*Aftermath cut*	*Cut at the end of the rains*	*Cut in the middle of the dry season*
Age when cut	*6 weeks*	*16 weeks*	*22 weeks*	*38 weeks*
	%	%	%	%
Crude protein .	10·48	8·00	7·33	5·18
Ether extract .	1·60	3·65	1·04	0·92
Crude fibre . .	31·40	33·35	37·09	39·72
Nitrogen-free extract . .	46·34	45·03	45·86	46·05
Total ash . .	10·18	9·97	8·68	8·13
Digestible crude protein . .	6·13	3·73	3·75	1·19
Starch equivalent .	35·80	29·16	23·75	18·01

nutrient changes in predominantly *Cynodon plectostachyum* hays made from comparable patches of herbage at different times of the year [2].

These figures indicate the changes to be expected, and emphasize the inferiority of current African practices of leaving the herbage crop uncut, to mature and dry off for dry-season consumption *in situ*. Apart from the wastage of nutrients in grazing such 'standing hays', due to their trampling and fouling by excreta, their nutritive values can drop to sub-maintenance levels, in keeping with general observations on liveweight losses, from about the middle of the dry season in semi-arid areas. Serious as the losses in digestible nutrients and starch-equivalent values are for such an accepted fodder as *Cynodon plectostachyum*, the decreases will be even more pronounced for the less leafy, harder and more stemmy species characteristic of the dry nomadic areas.

Louw [3] has reported a similar set of feeding values for grasses in a high-veld area of South Africa. His hays were made from herbage

TABLE 2. *Variations in Nutrient Values of South African Hays with Advancing Maturity* (Louw [3])

(*Dry-matter basis*)

		Age of herbage when cut for hay				
		1 month	*2 months*	*3 months*	*4 months*	*6 months*
1935–6	Digestible crude protein . .	6·61	5·34	3·55	2·27	. .
	Starch equivalent .	38·18	31·89	27·88	21·92	. .
1936–7	Digestible crude protein . .	5·07	3·96	3·17	1·98	1·42
	Starch equivalent .	38·92	35·98	32·54	26·04	22·11

collected from pure stands of *Cenchrus ciliaris*, *Chloris gayana*, *Digitaria pentzii*, *Panicum maximum*, and *Setaria lindenbergiana*, cut separately at monthly intervals but combined for the feeding trials (Table 2).

The starch-equivalent values of these South-African-grown hays agree closely with the Tanganyika figures, in spite of the differences between species, climatic and soil conditions, and a similar correspondence is apparent for the reductions in the digestible-crude-protein values with advancing maturity. Both sets of data emphasize the superiority of early-cut hays, observations entirely in agreement with experience from more temperate areas. In determining the most desirable age and stage of maturity for haymaking, the nutritive advantages of early cutting have to be set against the associated lower dry-matter yields at the earlier stage of maturity. Heavier yields of dry matter per acre are obtained with advancing maturity but the advantage in output is counteracted by decreasing nutritive values. This emphasizes the importance in semi-arid areas of deciding whether the aim is the conservation of the maximum quantity of nutrients from a given area or the preservation of fodders possessing the highest nutritive values. Undoubtedly cutting at an earlier stage of maturity must be employed if the hay is to contribute to the *production* part of a ration but, in African areas, the problem is only too frequently one of providing adequately for *maintenance* require-

TABLE 3. *Composition of Hays (percentages in dry matter)*

	Andropogon caricosus	*Cenchrus ciliaris*		*Chloris gayana*		*Cynodon plectostachyum*		*Digitaria pentzii*	*Panicum maximum*	*Pennesetum purpureum*
		Type B	Type D	First cut	After-math	First cut	After-math			
Height	2–2½ ft.	2½–3 ft.	2½–3 ft.	3 ft.	3 ft.	2 ft.	2 ft.	1 ft.	2½–3 ft.	2½–3 ft.
Maturity	Flowering	Flowering	Flowering	Flowering	Flowering	Early flowering	Early flowering	Early flowering	Not flowering	Not flowering
Crude protein	6·12	6·89	7·42	3·70	3·70	9·16	7·31	7·52	8·86	8·07
Ether extract	1·73	1·14	1·69	1·28	1·18	1·76	1·66	1·88	1·51	1·68
Nitrogen-free extract	40·08	42·82	43·96	42·83	44·43	43·44	44·12	44·09	44·22	45·26
Crude fibre	40·29	37·16	35·18	43·46	41·99	34·86	37·12	37·28	37·02	35·82
Total ash	11·78	11·99	11·75	8·73	8·70	10·78	9·79	9·23	8·39	9·17
SiO_2	7·96	6·90	7·97	4·95	5·26	5·57	5·28	5·22	4·56	5·27
SiO_2-free ash	3·82	5·09	3·78	3·78	3·44	5·21	4·51	4·01	3·83	3·90
Lime (CaO)	0·57	0·89	0·58	0·45	0·45	0·85	0·67	0·66	0·59	0·60
Phosphate (P_2O_5)	0·42	0·51	0·41	0·36	0·36	0·61	0·48	0·52	0·42	0·40
Potash (K_2O)	1·51	1·99	1·52	1·65	1·57	1·86	1·61	1·50	1·55	1·57
Soda (Na_2O)	0·25	0·25	0·24	0·26	0·21	0·25	0·23	0·22	0·22	0·23
Chlorine (Cl)	0·44	0·45	0·41	0·35	0·37	0·43	0·40	0·43	0·41	0·43

TABLE 4. *Percentage Digestibility and Nutritive Value of Hays (SiO_2-free dry-matter basis)*

	Andropogon caricosus	*Cenchrus ciliaris*		*Chloris gayana*		*Cynodon plectostachyum*		*Digitaria pentzii*	*Panicum maximum*	*Pennesetum purpureum*
		Type B	Type D	First cut	After-math	First cut	After-math			
Crude protein	42·63	43·90	49·26	29·41	29·55	59·06	49·89	56·00	50·12	53·34
Ether extract	60·13	30·58	42·77	39·00	36·51	51·01	41·05	55·76	49·99	54·31
Nitrogen-free extract	43·97	53·70	62·21	47·47	44·05	64·11	56·25	71·15	71·10	66·44
Crude fibre	56·48	64·17	65·85	53·00	52·60	63·35	59·33	59·22	58·86	60·11
Dry matter	51·44	57·99	61·49	48·56	40·97	62·81	57·68	64·51	61·84	64·08
Organic matter	49·93	57·05	62·19	49·12	47·27	63·04	56·70	64·68	63·25	62·54
Digestible crude protein	2·83	3·24	3·97	1·14	1·14	5·73	3·85	4·44	4·65	4·54
Starch-equivalent value	27·64	37·36	37·94	21·17	20·21	38·65	31·71	39·87	39·14	38·65

ments. Quite apart from the need already indicated for early grazing followed by a later closing of fields for haymaking, to prevent the coincidence of the proper stage of maturity with wet and unsuitable weather conditions, there is the further local problem of avoiding excessive lignification.

Materials and Methods

Table 3 shows the stage of maturity and the heights of the various grasses when they were cut for making into hay. After curing and collection, the materials were chaffed and stored in bags until the end of the green-grass season and then they were each fed independently to two mature native sheep. After a preliminary 8-day feeding period, 12-day collections of faeces were made and the digestibility coefficients and nutritive values were calculated. Kellner's [4] crude-fibre factors were used in the calculations of the starch-equivalent values and the results are summarized in Table 4 on a SiO_2-free dry-matter basis to eliminate the effects of the variable soil contamination. In order that a more accurate comparison could be made with the feeding values of the previously reported green grasses, the nutritive values of the latter have been recalculated on the basis of Kellner's crude-fibre correction factors and these results are shown together with the hay values in Table 5.

Discussion

Most species of East African grasses, even in their earlier stages of development, contain less digestible crude protein and have lower starch-equivalent values than the green herbage from grasses of comparable ages grown in temperate areas. The data in this and in a previous paper [1] illustrate the earlier crude-fibre development, while unpublished current work emphasizes the more rapid lignification of this fibre in local herbage than that which normally occurs in fodders from the temperate zones. By the time the haymaking stage is reached by the species in the latter regions, a higher crude-fibre content and a more advanced stage of lignification have been reached so that the differences in nutritive values, between such hays and those from certain locally grown herbages, are reduced.

The work of Woodman *et al.* [5, 6] suggests a more rapid and greater degree of lignification in British pastures whenever adverse climatic conditions, such as low winter temperatures or summer droughts, retard growth. The latter factor is obviously the more relevant under East African conditions and these British observations, on the lowering of the digestibility and the nutritive values of summer herbage, whenever lack of rain leads to an inadequate absorption of water and nutrients from the soil and to a desiccation of the herbage, are paralleled by East African observations. This reduction in feeding value is probably induced by an increased lignification of the cellulosic cellular structures —a morphological development which impedes the necessary close contact between digestive enzymes and rumenal bacteria with the intracellular constituents of the herbage. In East Africa the dominating local factors are too often the limitation of rainfall to restricted seasons and

TABLE 5. *Nutritive Values of Green Grasses and Hays (SiO_2-free dry-matter basis)*

Species and stage of maturity	*Nature of crop*	*Digestible crude protein*	*Starch equiv.*
Andropogon caricosus			
Flowering, up to 2½ ft.	Hay	2·8	27·6
Anthers emerged, leaves 1 ft., stems 2 ft.	Green aftermath	3·8	45·0
Cenchrus ciliaris			
Type B, flowering, up to 3 ft.	Hay	3·2	37·4
Type B, early flowering, up to 3 ft.	Green aftermath	6·0	51·2
Type D, anthers showing, 1–1½ ft.	Green first growth	8·2	54·0
Type D, early flowering, 2½–3 ft.	Green aftermath	8·8	52·7
Type D, flowering, 2½–3 ft.	Hay	4·0	37·9
Chloris gayana			
Early flowering, 1–1½ ft.	Green first growth	6·6	57·0
Early flowering, 1–1½ ft.	Green aftermath	4·4	43·2
Flowering, up to 3 ft.	Hay, first cut	1·1	21·2
Flowering, up to 3 ft.	Hay, aftermath	1·1	20·2
Cynodon plectostachyum			
Not flowering, 8–12 in.	Green first growth	15·3	54·7
Early flowering, 1–1½ ft.	Green aftermath	8·1	43·2
All stages of maturity, 2 ft.	Green growth	8·1	38·4
Early flowering, up to 2 ft.	Hay, first cut	5·7	38·6
Early flowering, up to 2 ft.	Hay, aftermath	3·8	31·7
Digitaria pentzii			
Not flowering, 4–6 in.	Green, first growth	11·7	61·0
Early flowering, 6–9 in.	Green, first growth	5·3	50·7
Early flowering, 12 in.	Hay, first cut	4·4	39·9
Anthers emerged, 10–12 in.	Green aftermath	3·7	40·7
Leerzia hexandra			
Not flowering, 6–10 in.	Green, first growth	7·0	51·7
Panicum maximum			
Type B, not flowering, 1–1½ ft.	Green, first growth	5·7	48·3
Type B, not flowering, 2½–3 ft.	Green, first growth	3·8	40·6
Type B, not flowering, 2½ ft.	Hay	4·6	39·1
Type B, early flowering, leaves 4 ft. stems 6 ft.	Green, first growth	2·7	32·2
Pennesetum purpureum			
Not flowering, 1–1½ ft.	Green, first growth	6·0	51·1
Not flowering, 2½–3 ft.	Green, first growth	4·9	40·8
Not flowering, 2½–3 ft.	Hay	4·5	38·6
Anthers emerged, up to 8 ft.	Green, first growth	3·5	31·8
Paspalum dilatatum			
Early flowering, 1 ft.	Green, first growth	3·3	52·2
Early flowering, 1 ft.	Green aftermath	3·3	54·0

the resulting influences thereof on soil moisture and soil-nutrient relationships. As soon as atmospheric humidities permit, the high local environmental temperatures encourage such rapid transpiration rates that frequent partial desiccations of the aerial herbage tissues are induced. Even in the rainy seasons, precipitation is frequently restricted to a short interval of the day while, during the remaining daylight hours, the heating from the sun's rays is so intense that the young grass may be constantly alternating between turgidity and partial flaccidity. With progress towards the subsequent non-rainy period, the intervals and the intensity of wilting increase, the crude-fibre and lignin contents rise but the digestibilities of the organic components in the herbage are decreased. This depression of digestibility often proceeds to the stage when the energy value derived from the soluble carbohydrates in the herbage becomes less than the corresponding quantity available from the crude-fibre fraction. A likely explanation of this anomalous condition would be the failure of the bacterial rumenal populations to break down the encrusting and more lignified cellular components sufficiently rapidly or completely to permit the subsequent full enzymatic digestion of their enclosed contents. However, whatever may be the true explanation, there can be no doubt that most local herbage species exhibit lower crude-protein but higher crude-fibre contents than fodders of the same age from temperate areas; comparable observations have also been reported from India [7, 8]. Such differences in composition affect nutritive values and a number of attempts have been made by workers in other areas to calculate nutritive values from regression equations and thereby avoid the need for time-consuming animal-digestibility studies [9, 10, 11].

Satisfactory regression equations have been developed for temperate-area species but, as pointed out by Watson [12], such equations do not necessarily apply to fodders from the semi-arid, sub-tropical zones. Duckworth [13] also investigated this divergence and produced highly significant but statistically different correlation coefficients between the crude fibre and the digestibility of the organic matter of fodders, as recorded with European and American cattle consuming temperate-area herbage, and Indian Zebu cattle consuming sub-tropical fodders. The scatter of the points in the diagram relating crude-fibre content with organic-matter digestibility was much greater and less precise for the Indian data. This is to be expected if, through unfavourable environmental conditions, lignification was more variable and occurred at an earlier age than is normal for herbage from temperate areas.

In the present series, certain local grasses, particularly the less leafy and more stemmy varieties, remained more fibrous than temperate species at all stages of maturity. This difference can be exaggerated in the cured hays if, through careless or incautious handling or because of excessive mechanical operations during unfavourable weather, the naturally small proportion of leafy material is reduced. This possibly occurred, in spite of the precautions to prevent it, with the *Chloris gayana* and the *Andropogon caricosus* hays and could have been a factor contributing to the feeding values of these hays being lower than might

have been expected. Such inadvertent losses are always more difficult to avoid with stemmy grasses containing relatively little leaf. The other hays compare favourably in starch-equivalent with medium- and good-quality products from temperate areas [4, 12, 14], but are slightly lower in digestible crude protein.

Unquestionably, the better qualities of such local hays could form exceedingly valuable supplements for the dry-season feeding of dairy cows, and of growing and fattening stock. In the European areas, hay-making is becoming increasingly popular and there is a recognized trade in hays for those farmers who feed intensively. Unfortunately, this conservational practice is but occasionally employed by the African owners of the vast majority of East African stock. Consequently, the traditional practice is for the animals to gain rapidly in weight on the lush pastures during the wet seasons and for this gain to be largely lost during the subsequent dry season [15]. The liveweight curve of most African-owned cattle is markedly undulating and therefore unnecessarily protracted so that, in spite of the limitations in available grazing, the quantity of herbage consumed for the production of a sizeable carcass is unnecessarily high. In the purely nomadic areas little can be hoped for in the way of herbage conservation, but in the more advanced agricultural areas the change from subsistence to productive farming is increasingly apparent and the need for a more rational system of animal husbandry is already being appreciated. Between these extremes, the communal herding system is still firmly entrenched and there is little hope of herbage conservation being practised for many years unless the stock owners, in these regions, see it being adopted in the more intensive areas and copy it from there.

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AN EXPERIMENTAL STUDY OF CERTAIN ASPECTS OF THE EPIDEMIOLOGY OF PARASITIC BRONCHITIS IN ADULT CATTLE

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Summary

Experiments are described which were designed to study the effect of certain husbandry practices on the severity of lungworm infection and to determine whether husk in older cattle was the outcome of a steady build-up of infection in the animals and on the pasture.

Bovines, ranging in age from 6 to 30 months, were exposed to lungworm infection under conditions of set stocking and rotational grazing. 'Understocked' was also compared with 'overstocked'.

In no case was a sustained rise in the faecal larval counts of the animals observed. The infections achieved in the test cattle were in no way referable to larvae which they themselves had passed.

Husk outbreaks in older cattle would appear to be the outcome of relatively sudden exposure to high levels of herbage infestation.

A comparison is made between the efficiency of different experimental treatments in the transmission of lungworm infection. No one system was consistently either more or less efficient in this regard than any other. The probable connexion between this and the finding that the infection is not built up over a long period of time is discussed.

THE urgent attention of helminthologists became directed to husk in adult cattle in 1951 when there was an apparent increase in its incidence. Whether this was due to an increase in correct diagnoses or to a true increase in incidence is difficult to determine. Many of the outbreaks studied in 1951 and in subsequent years [1] appeared to be associated in some way with the intensive grazing of clover leys. Such swards appear to be favourable to the transmission of lung-worm infection, assisting not only the translation of faecal larvae into herbage larvae but, presumably by providing a moist microclimate favouring the survival of the larvae, which are highly susceptible to desiccation [2].

The hypothesis was advanced by Taylor [3] that outbreaks of husk in adult cattle were the outcome of a build-up of infection as between the animals and the herbage. It was postulated that a group of cows would continue to reinfect themselves, by ingesting larvae which they themselves passed in ever increasing numbers, until their worm burden reached a point where the symptoms of disease appeared. It was suggested that the practice of strip grazing was particularly dangerous. In putting forward these suggestions, Taylor emphasized the need for experimentation.

A series of experiments was accordingly planned at the N.A.A.S. Experimental Husbandry Farm at Boxworth, which is situated on a stiff boulder clay west of Cambridge, to test this hypothesis. Strip grazing was

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compared with set stocking. In the first year also, chain harrowing was compared with no chain harrowing of the pasture, but subsequently this was discontinued and instead long herbage was compared with short. It was decided to attempt to achieve these differences in the length of herbage by means of the rate of stocking. Groups composed of equal numbers of cattle were grazed on plots of different areas. These differences in the rate of stocking admittedly introduced another variable, but one which could be allowed for by a simple arithmetical correction.

Experiment I. 1952

Strip grazing was compared with set stocking and chain harrowing with no treatment of the pasture. There were thus four treatments:

A. Rotationally grazed—harrowed. Five acres divided into six strips (A_1–A_6).
B. Rotationally grazed—not harrowed. Five acres divided into six strips (B_1–B_6).
C. Set stocking—harrowed. Nine acres.
D. Set stocking—not harrowed. Nine acres.

These plots were laid out on 'Side Hill', a cocksfoot—perennial ryegrass—white clover ley in its second year. This has been grazed in the spring by a group of cattle which were known to have been infected in the previous year. These animals could therefore be regarded as a potential source of infection and it was hoped that they would provide the initial infestation on the ground. The ground was then laid out into plots and twelve yearling cattle which had never been out at grass previously were assigned to each treatment and placed on the plots on 17 June. Samples of faeces and of herbage were taken on 25 June, 23 July, 20 August, 17 September, and 18 October. The samples of faeces were negative throughout for the presence of Dictyocaulus larvae but minimal numbers of larvae were recovered from the herbage of plots A_2 and D on 23 July, and from plots A_1 and C on 18 September. On 23 July all the cattle were coughing sufficiently to attract attention. Though subjective judgements are admittedly of very limited value, it was thought that, in so far as there was any difference, groups C and D coughed more frequently than the other two groups. Coughing subsided thereafter and none was heard in August and September, though an occasional cough was heard in October.

It appears that the animals which ran over the ground in the spring had indeed infected it. Not only did the animals cough but small numbers of larvae were recovered from the herbage. While the infection was thus present, it seems clear that it showed no signs of building up—in fact, it would appear that the light infections in the experimental cattle were spontaneously eliminated rather quickly. It has been the authors' experience that infections in older animals may be terminated before they become patent.

Experiment II. 1953

Rotational grazing was compared with set stocking as before, but instead of attempting to assess the effect of chain harrowing long herbage

was compared with short, field observations having continued to suggest that this factor might be of importance. Each group of animals consisted of fourteen head, but the area of the plots varied. The treatments were:

A.	Rotational grazing	short herbage	4 acres in six strips.
B.	,, ,,	long herbage	7 ,, ,,
C.	Set stocking	short herbage	5 acres.
D.	,,	long herbage	10 acres.

The field known as 'Bottom Thorofare' was used. This was a ley of cocksfoot, Timothy, meadow fescue, and white clover, in its fourth year.

In view of the experiences of 1952 it was decided to start with a higher initial level of pasture infestation. By introducing a source of infection only after the experimental animals had been on their plots for some

TABLE 1. *Faecal Larval Counts of 1953 Carrier Calves*
(larvae/10 gm. faeces)

Group	*Calf No.*	*30 June*	*8 July*	*14 July*	*Mean count over period 18 June–20 July*	*Mean count of faeces passed on to plot*	*Substitutions*
A	L505	36	35	4,110	434	237	Taken out 14·7
	L506	256	50	193			Put in 14·7
	L510	43	36	37	39·9		
B	L513	4	69	37	25·6	239	Taken out 14·7
	L515	22	233	3,660	452		Put in 14·7
	L508	102	144	319			
C	L509	263	69	2,080	707	456	..
	L512	31	67	603	194·6		
D	L507	261	7,600	4,612	2,475	1,649	Taken out 14·7
	L511	493	227	1,695			Put in 14·7
	L516	1	3,567	232	822		

time, it was hoped to determine what differences there were between treatments even if the infections did not steadily build up as between the experimental animals and the ground. Channel-Island calves born in March were experimentally infected with *Dictyocaulus viviparus*, 4,000 infective larvae being administered to each on 26 May. Two of these calves were put among the cattle on each treatment on 18 June, by which time the rotationally grazing groups, A and B, had been once round their six strips; groups C and D having been on their plots for an equal period. The artificially infected 'carrier' calves remained with their respective groups until 20 July, by which time groups A and B had completed their second circuit of the six strips.

The faecal larval counts of the carrier calves are shown in Table 1, which also gives details of the substitutions which it was necessary to make on account of the poor condition of some of the animals.

The experimental cattle were predominantly Friesian with a few Shorthorns. Of the fourteen animals of each group eleven were just under 18 months and three about 6 months old. The movements of the cattle, of groups A and B as also of the other groups, are shown in Fig. 1 in a diagrammatic shorthand notation. Plotted on a horizontal

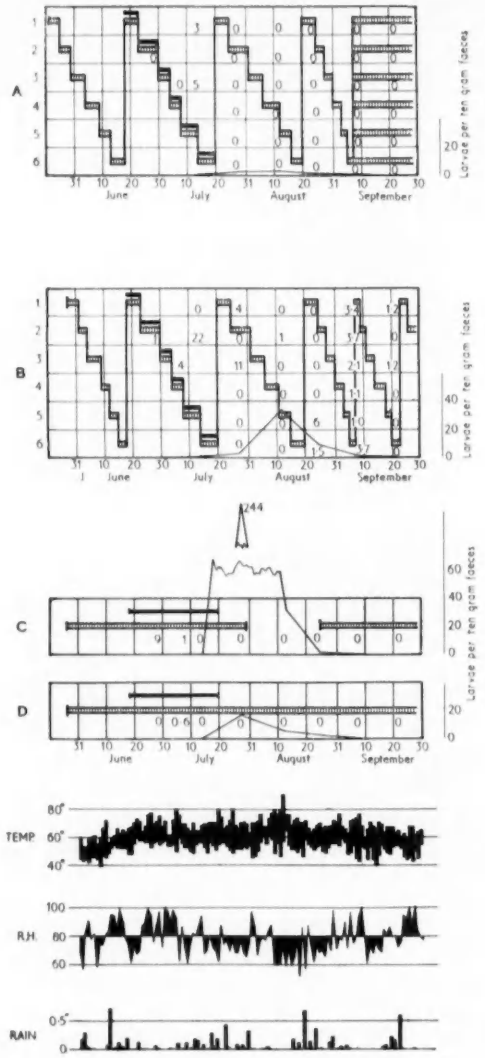

FIG. 1. *Summary of Experiment II*

Key to Figs. 1 *and* 2. The position of the experimental animals is shown by the broad striped horizontal line, that of the 'carrier' calves by the heavy black horizontal line. Mean faecal larval counts of the experimental cattle are plotted as graphs. The small numerals indicate the herbage infestation and represent the number of larvae recovered per pound of herbage. Below are plotted the daily readings of maximum and minimum temperature, relative humidity, and rainfall.

TABLE 2. *Faecal Larval Counts of 1953 Test Cattle*

(larvae/10 gm. faeces)

Animal No.	*Age in months*	30.VI	14.VII	28.VII	12.VIII	25.VIII	8.IX	22.IX
				Group A				
71	18	0	0	0	0	0	0	0
306	17	0	0	5	6	0	0	0
311	17	0	0	12	0	2	0	0
313	17	0	0	4	0	0	2	0
315	17	0	0	0	0	0	0	0
327	17	0	0	3	6	N.S.	1	0
332	17	0	0	0	4	1	0	0
355	16½	0	0	0	7	2	0	0
369	16½	0	0	0	1	0	0	0
372	16	0	0	5	0	3	0	0
395	14	0	0	0	4	1	0	0
447	7	0	0	0	11	0	0	0
484	8½	0	0	0	0	0	0	0
489	5	0	0	3	6	0	0	0
				Group B				
244	17½	0	0	0	0	0	0	0
299	17	0	0	0	0	0	2	0
314	17	0	0	7	0	0	0	0
329	17	0	0	0	0	0	0	0
348	16½	0	0	0	0	0	0	0
368	16½	0	0	13	6	0	2	0
375	16	0	0	0	0	12	0	0
376	16	0	0	2	10	N.S.	0	0
379	16	0	0	3	0	0	0	0
380	15	0	0	0	2	0	0	0
393	14	0	0	N.S.	1	0	0	0
469	6	0	1	0	22	36	0	0
486	5½	0	0	N.S.	0	22	0	0
491	5	0	0	7	425	50	1	0
				Group C				
72	18	0	0	0	1	0	0	0
298	17	0	0	0	0	0	0	0
303	17	0	0	7	32	2	0	0
305	17	0	0	4	7	0	0	0
321	17	0	0	1,720	100	0	0	0
325	17	0	0	0	0	0	0	0
355	16½	0	0	0	7	0	0	0
243	16½	0	0	0	0	0	0	0
367	16½	0	0	72	0	2	0	0
371	16	0	0	14	20	0	0	0
392	14	0	0	4	1	0	0	0
451	6	0	0	3	0	0	0	0
481	5½	0	0	1,550	230	7	2	0
488	5	0	0	39	48	0	0	0
				Group D				
304	17	0	0	N.S.	0	0	0	0
307	17	0	0	11	0	0	0	0
308	17	0	0	2	0	0	0	0
312	17	0	0	0	0	0	0	0
322	17	0	0	8	0	0	0	1
324	17	0	0	0	0	0	0	0
331	17	0	0	3	21	0	0	0
366	17	0	0	0	1	1	0	0
347	16½	0	0	0	0	0	0	0
370	16½	0	0	1	15	N.S.	0	0
396	14	0	0	24	6	0	0	0
449	6	0	0	60	4	7	0	0
458	6	0	0	57	22	27	0	0
494	5	0	0	43	9	0	0	0

time scale, the position of the experimental animals is indicated by a transversely striped horizontal line; that of the experimentally infected carrier calves by a heavy black horizontal line. It will be seen that towards the end of the season the time spent on each plot generally became shorter, and that on the 'A' plots the cattle were allowed to run over the whole area from 7 September onwards as there was not sufficient keep to make continued strip grazing possible.

The cattle of group C began to cough about the middle of July. The symptoms increased in severity and by 30 July there had been considerable loss of condition in all the cattle of the group and some were showing signs of respiratory distress. It was decided, therefore, to house these animals and they were taken into a half-covered yard. The symptoms now abated rapidly and on 25 August the six strongest, Nos. 298, 243, 325, 371, 305, and 303 were put back on C plot.

The animals of group D also began to cough in the middle of July, but only mildly. No more severe symptoms developed except with one animal, No. 458, which was housed on 30 July.

Groups A and B began to cough a fortnight later than groups C and D, but here the symptoms were extremely slight and only of short duration.

The individual faecal larval counts of the experimental animals are shown in Table 2.

The means are plotted in Fig. 1. It will be seen that the first positive counts were obtained at the same time in all four groups although the peak in the set-stocking groups came sooner than in the strip-grazing groups. It would follow that the strip-grazing cattle must have begun to acquire their infections before the beginning of July and that the peak was due to infection picked up not later than 20 July. It is safe to say, therefore, that in the strip-grazing groups the infections were acquired while the experimentally infected calves were on the plots. The time taken for the larvae of *D. viviparus* to reach the infective stage is only five days under good conditions and on three occasions the cattle were on a single strip longer than this. There were also other opportunities for infection during the period that the carrier calves were on the strips; not only could the cattle reach the preceding strip through the electric fence, but all the strips of each rotationally grazed area opened into a common corridor by means of which the animals had access to water.

The form of the infection in all four groups was the same. The faecal larval counts rose fairly rapidly to a peak and as rapidly fell away again. Consideration of the graphs of faecal larval counts will show that the infections were entirely referable to larvae passed by the carrier calves and that the infections were not augmented by the uptake of larvae passed by the experimental animals themselves.

A point of some interest is that in all the groups, even in C, the faecal larval counts of a number of individuals remained negative throughout. This cannot have been because these animals did not pick up the infection. As has already been mentioned, the infection in older animals may be spontaneously terminated before it becomes patent.

Estimations of pasture infestation were carried out periodically, first

on selected strips and subsequently on every strip. The results of these estimations are shown in Fig. 1 as small numerals representing the number of larvae recovered per pound of herbage. It will be seen that a high count was recorded on C on 29 June and it is to this that the high infections acquired by the animals of C were due.

On B high levels of pasture infestation were evidently reached in July, but these had materially decreased by the time the cattle returned. These herbage infestations were due to larvae passed by the carrier calves. The larvae passed by the experimental cattle themselves were not reflected in the herbage infestation counts until the end of August, by which time the infections in the experimental cattle had been almost terminated.

Experiment III. 1954

In 1954 an attempt was made to limit the transmission of infection on the rotationally grazed groups during the time that the carrier calves were on the plots. The cattle followed a strict rotation, remaining for exactly 4 days on each of the four plots. In addition to this there was no corridor, and water tanks were moved from strip to strip with the cattle.

These precautions were perhaps of rather limited value since it was necessary to use animals which had been out at grass before, and even a number which had been in the 1953 experiment. These latter were chosen from animals of Groups A, B, and D of 1953, from the faeces of which no lung-worm larvae had ever been recovered in that year. It was known that these might act as a source of infection and indeed, as described below, two animals were subsequently demonstrated to be acting in this manner.

The same field was used as in 1953, but the areas of the plots were altered slightly, since it was found that the original area of C had not been entirely adequate to support the cattle. The areas in 1954 were: A—4 acres; B—7 acres; C—5·5 acres; D—9·5 acres. With this arrangement the areas of A and B were in the same proportion as those of C and D.

The experimentally infected carrier calves, which had each received an oral dose of 3,500 *D. viviparus* larvae on 26 April, were put on to the plots on 14 June, by which time the rotationally grazing animals had made one complete circuit of their six strips. It had originally been intended to put both these and the experimental cattle out earlier, but the weather had prevented this. As will be seen from Table 3, the faecal larval counts of the carriers were declining by the time they were put out. The carrier calves remained with their respective groups for 24 days, the time taken for the rotationally grazing groups to complete their second circuit.

The movements of animals are shown in Fig. 2, in which the results of the experiment are also summarized.

The experimental cattle were all Friesian steers. Each group consisted of thirteen animals, of which three had been in groups A, B, or D of the previous year's experiment and were between 29 and 30 months old. Between three and five, aged from 15 to 29 months, had been out at grass in the previous year but had shown no symptoms of parasitic

bronchitis and the remainder had not been outside before and were between 5 and 12½ months old.

The symptoms of husk which developed were not very severe. Coughing was most pronounced in groups B and C and started about the middle of July. The faecal larval counts of the experimental cattle are shown in Table 4.

It will be seen that two animals that had been out at grass before were passing larvae in June. Neither of these animals had shown noticeable symptoms of husk in the previous year and of one it was known that regular examinations of faeces samples by an uncommonly sensitive

TABLE 3. *Faecal Larval Counts of 1954 Carrier Calves*

(larvae/10 gm. faeces)

Group	*Calf No.*	*29 May*	*31 May*	*15 June*	*23 June*	*30 June*	*12 July*	*Mean over period 14 June–7 July*	*Mean count of faeces passed on to Plot*	*Substitutions*
605	A	146	824	88	1	0	0	21·6	13·4	..
610		181	294	11	0	0	18	5·2		
600	B	20	286	203	17	0	0	49·8	24·9	..
603		5	1	0	0	0	0	0		
606	C	622	410	524	134	246	85	252	127·7	Taken out 29.6
608		1,408	N.S.	21	0	..	..	3·4		Put in 29.6
611		5	N.S.	N.S.	0	0	0			
604	D	145	104	11	0	0	15	4	24·7	..
607		2,160	1,092	93	N.S.	16	4	45·3		

technique had failed to demonstrate the presence of larvae. This observation is of interest in confirming the suggestion [4] that animals that have at some time been exposed to infection subsequently represent a potential source of infection. Only two of these animals were actually caught in the act of passing larvae. The possibility cannot be excluded that others did also, since it appears that carrier animals of this type may pass larvae for only short periods at a time.

Certainly, the rotationally grazing animals did pick up a few larvae before their third circuit of the strips; the positive counts obtained on 14 July, in animals which had never been out at grass before, must have been due to infection acquired before 23 June. This may have been due to some of the older animals acting as a source of infection, or to the animals grazing the strip that they had just left, through the fence, even though two electrified strands were used. The peak of faecal larval counts appeared rather later in the rotationally grazing cattle than in those on set stocking, and appears to have been due to infection acquired when the animals returned to their strips the third time, that is to say

TABLE 4. *Faecal Larval Counts of 1954 Test Cattle*

(larvae/10 gm. faeces)

Group A

Animal No.	*Age in months*	23.VI	14.VII	28.VII	11.VIII	26.VIII	8.IX	22.IX	7.X	19.X
244	30	0	0	0	0	0	0	0	0	0
347	29	0	3	0	0	0	0	0	0	0
348	29	0	0	0	0	0	0	0	0	0
310	29	0	0	0	0	0	0	0	0	0
349	28½	0	0	0	1	0	0	0	0	0
365	28½	39	0	0	0	0	0	0	0	0
519	11½	0	0	1	0	0	0	0	0	0
521	9	0	0	0	0	0	0	0	0	0
547	7½	0	0	4	54	0	0	0	0	0
549	7½	0	33	0	72	149	0	3	0	0
564	6½	0	0	0	0	0	0	5	0	0
569	6½	0	0	10	20	63	85	0	N.S.	0
588	5	0	93	238	54	139	19	21	0	1
			0	0	14	39	97	31	175	19

Group B

71	30	0	0	0	0	0	0	0	0	0
298	29½	0	0	0	0	0	0	0	0	0
315	29½	0	0	0	0	0	0	0	0	0
317	29	0	0	0	0	0	0	0	0	0
345	29	0	0	0	3	0	0	0	0	0
374	28	0	0	0	0	0	0	0	0	0
518	12½	0	0	0	0	0	0	0	0	0
524	8½	0	0	4	27	0	0	0	0	1
536	7½	0	6	0	137	3	0	0	0	0
539	7½	0	0	1,176	1,902	377	7	64	139	144
563	6½	0	0	7	17	0	0	0	0	0
585	5	0	44	0	108	0	0	0	0	0
594	4½	0	0	195	119	63	40	0	0	0
				0	22	0	3	0	0	0

Group C

304	29	0	0	1	0	0	0	34	0	0
312	29½	0	0	0	0	0	0	0	0	0
324	29	0	0	0	0	0	0	0	0	0
336	28½	0	0	0	0	0	0	0	0	0
356	28½	0	0	0	0	0	0	0	0	0
500	16	0	9	112	17	0	0	0	0	0
501	16	0	6	3	0	0	0	0	0	0
503	15½	0	17	N.S.	71	7	2	0	0	0
533	7½	0	0	611	40	51	4	0	2	0
540	7½	0	198	238	306	270	59	3	2	0
558	7	0	0	47	200	40	96	0	0	0
580	5½	0	27	379	372	53	24	0	3	0
587	5	0	0	4	14	22	0	0	0	0

Group D

325	29	0	13	0	0	0	0	0	0	0
329	29	186	0	0	0	0	0	0	0	0
484	17½	0	0	0	0	0	0	0	0	0
326	29	0	0	1	0	0	0	0	N.S.	0
351	28½	0	0	0	0	0	0	0	0	0
364	28½	0	8	0	0	0	0	0	0	0
446	18½	0	N.S.	5	2	0	3	0	0	0
526	8½	0	0	0	8	2	0	0	0	0
535	7½	0	0	0	2	0	0	0	0	0
557	7	0	5	0	0	0	184	12	0	2
565	6½	0	0	25	60	63	0	10	0	0
579	5½	0	0	26	206	21	5	4	0	0
590	5	6	4	5	14	16	42	0	0	0

the time after the carrier calves were with them. It will be seen that the greatest infections were established in the animals of groups B and C.

The indexes of herbage infestation recorded in Fig. 2 show that no measurable infestation was achieved on C and D. High levels were seen on A and B, but by the time the animals returned, the level of infestation had dropped considerably, to a point where it was no longer dangerous. It would appear, however, from the effect on the animals, that survival of larvae in the long herbage of B was rather better than on A.

As will be seen from Fig. 2, the larvae passed by the experimental cattle were not reflected in a rise in herbage infestation until after the peak of faecal larval counts had been passed and the infections in the animals were declining.

Towards the end of the season symptoms of parasitic gastritis appeared in some of the animals, and five, Nos. 588, 536, 580, 446, and 579, were seriously affected. It will be seen by reference to Table 4 that the tendency for the mean larval counts of groups A and B to remain positive in October was entirely due to two of these animals.

Discussion

In all three experiments there was no evidence of a continued rise in the infestations, either in the animals or on the herbage. In the second and third experiments the faecal larval counts of the experimental animals rose and fell rapidly and it would appear that by the time the number of larvae which they passed was reflected in a rise in the herbage infestation, the experimental cattle were already refractory to reinfection.

Whether the infection in group C, which had to be removed from their plot, would have continued to rise had they been left on the plot is perhaps open to question, but there can be no doubt that the appearance of serious symptoms was the outcome of relatively sudden exposure to a high level of herbage infestation. It is quite clear that there was not in this case a gradual build-up of infection which resulted in the appearance of symptoms when the worm burden ultimately became excessive.

The infections which were achieved in the test cattle in both 1953 and 1954 were entirely referable, as may be seen from Figs. 1 and 2, to the herbage infestations due to the larvae passed by the artificially infected carrier calves. It appears that older animals acquire an effective resistance rapidly. Not only is the infection rapidly terminated, but such larvae as they ingest, even a relatively short time after first exposure to infection, do not become established. Certainly, in these experiments, by the time the larvae passed by the test cattle appeared on the herbage, the test cattle themselves were refractory to reinfection. The process operative in these experiments was simply the transmission of infection from the carrier calves to the test cattle.

It is possible, therefore, to consider the various treatments in the light of their efficiency as means for the transmission of lung-worms. A comparison of this efficiency of the various treatments is made in Table 5. In this a 'transmission coefficient' has been calculated which is a measure of the infections established in the test cattle per unit of infection

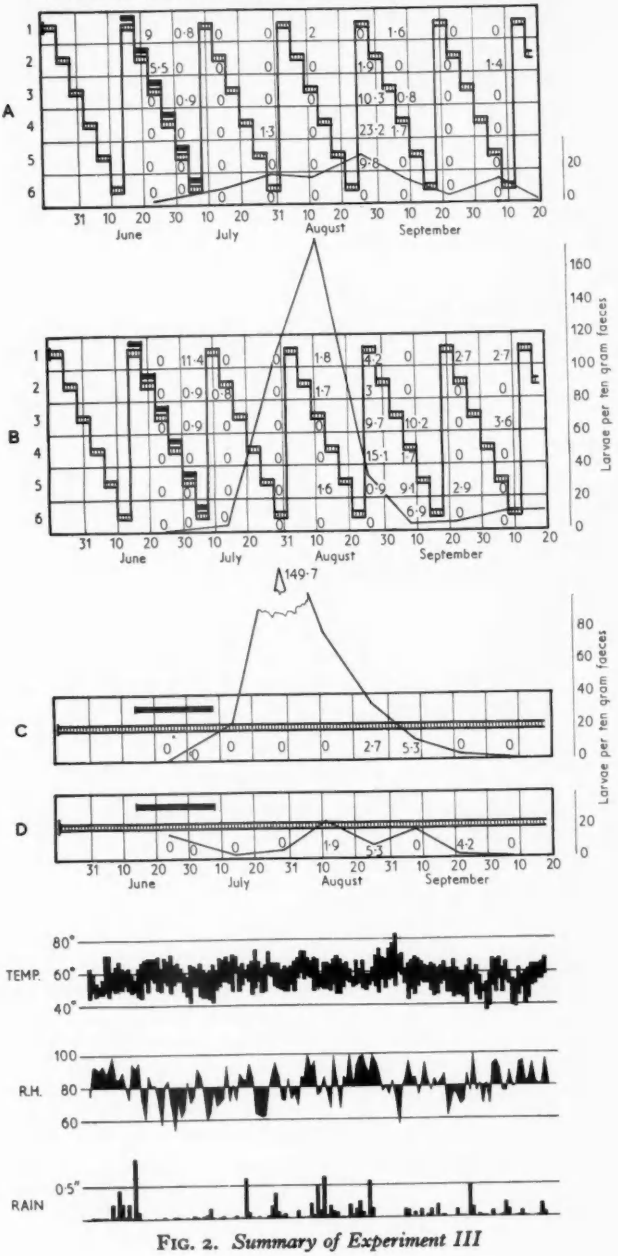

FIG. 2. *Summary of Experiment III*

deposited by the carrier calves. A 'corrected transmission coefficient' has also been calculated, which indicates what the 'transmission coefficient' would have been if the density of stocking had been the same on all the treatments and the differences in the length of herbage had been brought about by some other cause.

TABLE 5. *Comparison of the Efficiency of the Treatments in the Transmission of Lung-worm Infection*

Plot	*I. Mean of three highest mean faecal larval counts of test cattle*	*II. Mean carrier calf faecal larval count*	*III. No. of days carrier calves on plot*	*IV. Area grazed, in acres*	*Transmission coefficient* $\frac{1{,}000 \times I}{II \times III}$	*Order of magnitude*	*Corrected transmission coefficient* $\frac{100 \times I \times IV}{II \times III}$	*Order of magnitude*
1953								
A	2·1	237	32	4	0·28	3	0·11	4
B	9·1	139	32	7	1·19	2	0·83	2
C	92·2	456	32	5	6·3	1	3·1	1
D	8·2	1,649	32	10	0·16	4	0·16	3
1954								
A	22	13·4	24	4	69·0	2	27·6	3
B6	106·3	24·9	24	7	178·0	1	124·6	1
C	87·3	127·7	24	5·45	24·0	4	13·1	4
D	35	24·7	24	9·55	59·0	3	56·3	2

It will be seen that if these coefficients are arranged in order of magnitude as shown in Table 5, the order in 1953 is different from that in 1954. Some light may be thrown on this inconsistency by a consideration of the factors which determine the effect of the methods of management that were compared. The density of stocking may affect the transmission of lung-worms in two ways. On the more lightly stocked area there will be a greater quantity of herbage and the larvae will be diluted by this. On the other hand, the greater bulk of herbage will provide more favourable conditions for the larvae by protecting them against desiccation. These two component factors are therefore antagonistic and their relative importance depends among other things on climatic conditions.

A high rate of stocking alone does not of itself imply a greater risk of helminthiasis. What is significant in the production of disease is the number of infective larvae ingested by the animal or, as is suggested by the results of Michel and Parfitt [5], the concentration of larvae on the herbage. Other factors apart, it matters little whether the quantity of herbage in which a given number of larvae are to be suspended is growing on a large or on a small area. When the rate of stocking is high, with the consequence that the herbage is short and the larvae are therefore suspended in a small weight of herbage, then this will tend to produce a high concentration of larvae. On the other hand, the short herbage will not provide such favourable conditions for the survival of the larvae, which are more likely to be exposed to desiccation. Indeed, this effect

may well outweigh that of the lesser dilution unless climatic conditions provide the required high humidity in the short grass.

The comparison of rotational grazing with set stocking is likewise influenced by two antagonistic factors. In both set stocking and rotational grazing, provided that the larval output of the calves remains constant, the same total number of larvae are deposited on the entire area during the period that the rotationally grazing animals complete one circuit of all the strips. In the case of rotational grazing, however, each strip receives its full quota of larvae over a short period, so that all these larvae may contribute to the resulting herbage infestation. Under conditions of set stocking, on the other hand, each portion of the field receives its quota of larvae, not at once but over a period of weeks. Since the larvae begin to die off immediately, the herbage infestation which is established in these circumstances can never be so high as that under conditions of rotational grazing.

On the other hand, while the animals are immediately exposed to the lower herbage infestation that is achieved on the set stocking, they are not exposed to the higher herbage infestation which results on the rotationally grazed strips until some time later, by which time that higher herbage infestation has fallen. The relative merits of the two systems of grazing depend therefore on the translation of faecal larvae into herbage larvae and on the survival of the larvae. Thus, if conditions for translation are particularly good, the animals grazing under conditions of set stocking may be exposed to a high herbage infestation. On the other hand, particularly favourable conditions for survival will lead the rotationally grazing animals to return to herbage infestations that are still high.

The comparisons made in these experiments, therefore, are each concerned with an equilibrium between the effects of antagonistic factors. This equilibrium, however, is unstable, being determined by climatic and other adventitious factors whose incidence is at random. In consequence, any differential effect on the incidence or severity of husk which could result from the methods of management compared might have become manifest only over a long period of time. As has been shown, the process involved is the transmission of infection from one set of animals to another and the relevant portion of this process occupies only a short period of time. It would follow that the effect of the treatments is at most a slight one, which might become manifest, over a period of years, in the relative number of occasions on which husk outbreaks occur under the different methods of management. While these general considerations help to explain the different results obtained in 1953 and 1954, the more detailed search for immediate causes is much more difficult.

In 1953 a high herbage infestation appeared on C for a short time, but this sufficed to determine the pattern of events. The cattle on B in that year must have met some appreciable herbage infestations on their third circuit of the strips, but it would appear that they had already experienced infection on their second circuit and had derived some resistance from this. In all three years it was clear that it is the level of infestation to

which the animals are first exposed that is of importance and it is highly probable that relatively sudden exposure to heavy infection is required to produce husk in older animals.

In 1954 the rotationally grazing animals again became infected before their third circuit of the strips, in spite of the efforts made to prevent this. None the less, the transmission of infection was most effective on B, no positive herbage count being recorded from C. The causes of the appearance of a high infestation on the herbage of C in one year but not in the next year, though the circumstances were similar, are surely complex, and climatic factors are certainly of importance. For this reason certain meteorological data are shown in Figs. 1 and 2. While it is tempting to draw conclusions as to the relationship between climatic factors and the translation of faecal larvae into herbage larvae, a great many more observations on this matter are needed before suggestions can properly be made.

The point which has been discussed above in general terms, that higher herbage infestations result on the rotationally grazed plots than on those grazed under conditions of set stocking, is well illustrated by the results obtained. In 1954 this phenomenon was augmented by the circumstance that the larval output of the carrier calves was not uniform over the entire period, almost all the larvae being passed on to the first two or three strips. This is clearly seen from the indices of herbage infestation shown on Fig. 2.

It should perhaps be emphasized that the results obtained and the considerations that have been discussed apply properly only when animals of the ages used in these experiments are concerned. It might be of interest to determine whether the use of younger animals in such experiments would materially influence the type of result obtained.

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A STUDY OF SOIL FERTILITY IN ZANDELAND

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Summary

The results of a study of soil fertility over six years (1949–55) at the Yambio Experimental Farm on the Nile–Congo divide are reported and considered in comparison with the results of peasant practice. Practically no scientific data are available on the soils and agronomy of this region.

The different factors of climate, geology, and vegetation are briefly considered in relation to soil formation. Although in general lateritic soils are of low nutrient status it is not always appreciated that they are nevertheless capable of considerable cropping capacity when rightly managed.

The location and cropping in the field trials were representative of the agricultural soils and native crops of the Yambio district. Data on crop yields, rotations, soils, and vegetative regeneration are recorded over the period of six years.

Yields of groundnuts and of eleusine revealed a marked decline in the fourth year of the cropping rotation, falling further to negligible yields in the sixth year. Although the yield of cotton also fell after three years, an economic level was still maintained thereafter into the sixth year. These data indicate that Station yields are almost invariably higher than those obtained by the local cultivators, for the first three years, but that economic yields are no longer produced after three to four years' cropping. Cotton was shown to be more resistant to low-fertility soil conditions than either groundnuts or eleusine. The higher yields obtained at the Station are considered to be the result of the maintenance of higher standards of crop husbandry.

Some characteristics of the agricultural soils of this region are summarized and field notes of representative profiles from four blocks of the experiment are included.

Soil analyses were made at the beginning and end of the experiment. The analytical results at the end of the six-year period showed that differences between the nitrogen content of the soil from the plots under the different treatments were not striking. Progressively lower values for total nitrogen with increasing periods of continuous cropping were clearly shown on two blocks, but not on another block with a high incidence of pea-iron gravel with hard laterite exposed close to the surface. It is noteworthy that on such soils shallow profiles (i.e. down to the pea-iron gravel layer) often reveal a high nitrogen content and may exhibit a high level of crop production. A significant correlation was demonstrated between the total nitrogen and the exchangeable calcium in the soil samples examined.

The falling-off of yields of groundnuts and eleusine to uneconomic levels after the third year of continuous rotational cropping, to a level amounting to practically complete crop failure in the sixth year, is a clear vindication of the local practice of bush fallowing after two or three years' cropping (in the absence of fertility recuperative treatments), but the soil data obtained in this study strongly discount the possibility that this decline in yield is caused by exhaustion of soil nitrogen.

The study concluded with an analysis of vegetation regeneration after cropping. After two years' cropping, bush regeneration in the fallows was rapid and grass species were rapidly suppressed. With four and six years' cropping, the stump population suffered some mortality. *Imperata cylindrica* dominated the fallow in the early years and after four years' cultivation regeneration of woody species can be expected to be slow.

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THIS paper records the results of a preliminary study of soil fertility and crop production carried out at the Yambio Experimental Farm during the years 1949–55. As originally planned in 1949, a trial consisting of a series of observation plots was designed with the object of providing early information on the duration and level of yield, with subsequent bush-fallow regeneration, on some characteristic soil types. Differences in the soil-nutrient status, following different treatments, could be studied at the conclusion of the trial. These preliminary experiments were intended to be the forerunners of a more detailed and conventional investigation. Since by unavoidable circumstance it was no longer possible to carry out this planned research programme, it was decided to put on record some results and conclusions reached so far, which might be of more than local value.

The location of the Station is 730 metres above sea-level in N. Lat. 4° 34′; E. Long. 28° 24′ on the Nile–Congo divide in the Zande district of Equatoria Province, Sudan. The average rainfall at the Station for the period under review was 1,450 mm. with an average of 130 days of measurable precipitation per annum. Although the rainfall is comparatively high the distribution is not always even. Two slight peaks are discernible in May and August. There is a three months' dry season of varying intensity, December to February. The mean daily maximum temperature ranges between 28·5° C. and 34° C. and the mean minimum between 16° C. and 19·5° C.

The topography of the district is gently undulating and for the greater part it is covered with Combretaceous grass woodland. Species are too numerous to be listed in detail but amongst the more important savannah species are the following: *Anogeissus schimperi.*, *Terminalia* spp., *Vitex cuneata*, *Acacia* spp., *Annona senegalensis*, *Grewia mollis*, and *Nauclea latifolia*. Grasses include *Hyparrhenia* spp., *Panicum maximum*, *Rottboellia exaltata*, and *Imperata cylindrica*. Gallery forests follow steep-sided stream banks and some typical species include: *Khaya grandifoliola*, *Erythrophleum guineense*, *Albizzia coriaria*, and *Sysygium owariense*. Near Yambio and elsewhere on the divide the occasional remains of High Forest are still in evidence and it is probable that this was the climax vegetation in recent times. An important feature is the fact that the whole character of the vegetative cover has been virtually changed by the effects of fire and to a much lesser extent by cultivation. Savannah trees show varying degrees of fire tolerance.

Geologically the district forms part of the basement complex which represents two-thirds of the rock exposures of the Sudan. Andrew [1] considers the basement complex of southern Sudan to consist of a peculiar group of highly crystalline granoblastic-foliated basic to acid gneisses with hypersthene and transparent felspar intruded into foliated paraschists and paragneisses. The hypersthene gneisses belong to the charnockite series also occurring in northern Uganda. This basement complex represents most of the hills and peneplains of Equatoria west of the Nile. The area is much dissected by small perennial streams flowing northward ultimately to join the Bahr el Ghazal or to be lost in the swamps of the Sudd.

The extensive deposits of mid-Tertiary ironstone were derived by

weathering and leaching of the local rocks, i.e. from the crystalline basement complex and are clearly *in situ*. The ferruginous clays underlying the ironstone duricrust frequently contain vestiges of the rock-structure undisturbed. In certain cases this is also true of the laterite itself. Andrew (*loc. cit.*) attributes the red loams and unconsolidated ferruginous clays of western Equatoria, usually containing pisolithic concretions, to a later Pleistocene lateritic phase, and similarly *in situ*. This is not to be confused with the older mid-Tertiary laterite. Much of the parent material from which a soil develops is unconsolidated and weathered and it is emphasized that the climatic conditions, under which such weathering took place, were not necessarily those of today. Inevitably much more theorizing than experiment has been evident in the effort to relate soil formation with geology, climate, and topography.

Although the lateritic soils of this region are in general of low nutrient status, when properly managed they are nevertheless capable of considerable crop productivity. Otherwise, the indigenous tribesmen relying on these soils for their subsistence crops could never have survived. Gourou [2] would appear to express a somewhat extreme viewpoint in his anxiety to stress the inherent incapacity of lateritic soils and the 'utter infertility' of laterite itself. In some respects the situation thus depicted does not appear to be in accordance with the facts observed in the field. It is important to bear in mind also that under certain conditions of climate, vegetation, and topography lateritic formations are capable of a gradual break-down into soil by the slow process of weathering. Moreover, whatever the explanation, better annual crops are sometimes produced on soils with a high content of pea-iron gravel (pisoliths) in which occur outcrops of laterite rock. Most of the agricultural soils of the Zande district consist of ferruginous loams and sandy loams, with good crumb structure. A typical profile shows a thin layer of leaf litter with a dark-brown top soil extending to about one foot with a uniformly red-clay subsoil containing varying amounts of pea-iron gravel. This horizon then passes into the characteristic mottled zone, but the parent material or virgin rock is not usually exposed except in very deep profiles.

The country is inhabited by the Azande tribes, of mixed Sudanic and Bantu origin, who practise shifting agriculture and the annual burn, cultivating the land normally for two to three years before allowing it to revert to bush fallow. The staple food crops are groundnuts (*Arachis hypogaea* L.), eleusine (*E. coracana* Gaertn.), cassava (*Manihot utilissima* Pohl), sesame (*Sesamum orientale* L.), and maize (*Zea Mays* L.). Other food crops include sorghums, grams, bananas, and mangoes. The main cash crop is a variety of American upland cotton (*Gossypium hirsutum* L.). Being situated in the fly belt, animal husbandry as yet forms no part of the agricultural system in Zandeland and meat is usually obtained by hunting. Hunting fires, often late in the dry season, exercise a profound effect on the soil and vegetation.

Layout of Trials

A strip of land 1,250 × 50 metres was divided into twenty-five blocks, each 50 metres square. Two blocks were atypical, being situated on a

noritic outcrop. The rest were sited over a hill-top on a line at right angles to the contour, the last block (No. 25) being on the edge of gallery forest. Typical soil profiles taken in the blocks are described later. All blocks were cleared of vegetation in March 1949. Grass was hoed, bush cut, trees stumped to 1 metre high, the movable timber being removed, and the site burnt. Each block was then divided into sixteen plots, each 12·5 metres square, and at the time of first opening, the seven plots on two adjacent sides of each block were allowed to revert to bush. The remainder of each block, comprising a square of nine plots, was divided into three sets of three plots, forming three strips, each of which ran at right angles to the contour. One strip was allotted to each of three rotations, A, B, and C. The allocation of rotations varied systematically and not at random.

TABLE 1. *Rotations*

Year	A	B	C
1949	Cotton	Groundnuts/Eleusine	Maize/Eleusine
1950	Groundnuts/Eleusine	Cotton	Cotton
1951	Cotton	Sesame	Groundnuts/Eleusine
1952	Groundnuts/Eleusine	Laginaria/Eleusine	Cotton
1953	Cotton	Sesame	Groundnuts/Eleusine
1954	Groundnuts/Eleusine	Sesame	Cotton

Of the three plots into which each strip was divided, one plot was allowed to revert to bush after cropping for two years, the next after cropping for four years, the third after cropping for six years. The plots cropped for two years were in line alongside three end plots receiving no cultivation. Then came the plots cultivated for four years, with the plots cultivated for six years occupying three end plots. These four *duration-of-cropping treatments* are referred to subsequently as uncropped, two-year cropping, four-year cropping, and six-year cropping.

Rotation B was utilized for observing the behaviour of minor crops and in this paper only the three main crops, groundnuts, eleusine following groundnuts, and cotton, are considered in some detail. Groundnuts, bunch type, were sown in the third week of April at a spacing 33·3 × 33·3 cm. Eleusine was broadcast at the time of harvesting groundnuts so as to obtain a stand with 15–20 cm. between plants. The period from sowing to maturity averaged 95 days for groundnuts and 120 days for eleusine. American upland cotton was sown at a spacing 90 × 30 cm. in mid-June and thinned to two plants per hole. Dependent on season and crop, a standard of six pickings at 10-day intervals, beginning 140 days after sowing, was adopted. Plot size after discarding borders was 100 square metres. For rotations A and C nine crops were thus taken off the land in the six-years' cropping treatment, and for rotation B eight crops.

Crop Yields

The approximate levels of yield expected at the Station for the three crops under consideration are given in Table 2. Higher standards of cultivation have resulted in a level of yields higher than that obtained

by the peasant cultivator. In the specific case of cotton the difference between precept and practice was startling. In seasons 1952 and 1954 the average yield for the district was less than one-quarter of that of control plots on first- and second-year land at the Station and in 1953 slightly less than half.

TABLE 2. *Approximate Levels of Yield of Cotton, Groundnuts, and Eleusine expected at the Station*

*Rotls per feddan**

	Seed cotton	*Unshelled groundnuts*	*Eleusine grain*
Average . .	600	800	900
Good . . .	800	1,000	1,100
Excellent . .	1,000	1,200	1,300

The average yields of cotton, groundnuts, and eleusine obtained in the trial, from rotations A and C, are summarized in Table 3. As groundnuts followed by eleusine do not occur in the first year of rotations A and C, the yields of these crops in rotation B are given for 1949. For comparison, average cotton yields at the Station on control plots of other experiments on first- and second-year land after bush fallow are included.

TABLE 3. *Average Yields for all Blocks*

*Rotls per feddan**

Cultivation period (years)	*Year*	*Seed cotton*	*Unshelled groundnuts*	*Eleusine grain*	*Seed cotton (Station average)*
2	1949	997	721	994	840
	1950	1,074	1,127	1,204	900
4	1949	1,029	795	1,010	840
	1950	1,080	1,240	1,194	900
	1951	620	800	1,275	530
	1952	670	565	411	960
6	1949	1,067	831	1,067	840
	1950	1,171	1,144	1,163	900
	1951	604	965	1,272	530
	1952	719	505	397	960
	1953	448	186	257	790
	1954	496	..†	12	930

Cotton yields for the six-year-cropping treatment, expressed as percentages of the average Station yields in the same years for control plots on first- and second-year land after bush fallow, and for the cotton observation plots, are given in Table 4. The latter plots, laid down in 1951, were sited on comparatively poor land and the level of yields has been uniformly low.

* One rotl = 0·99 lb. One feddan = 1·038 acres. One rotl per feddan (r.p.f.) = 1 lb. per acre (approx.).

† Damaged by wild pig.

For the first three years of cropping, cotton yields were above the Station average. The fourth year showed a decline in yield and in the fifth year the crop looked poor from the beginning. Stand was good but vegetative growth was weakly. The final height for all the plots averaged only 50 cm. compared with 100 cm. overall average for the good 1950 crop, and there was further loss in productivity. In the sixth year the crop was again vegetatively poor with an average plant height of 60 cm. The yield, although higher than in the previous season, showed a further decline when the seasonal effect is taken into consideration (i.e. in comparison with the Station average).

TABLE 4. *Cotton Yields as Percentages of Average Station Yield and of Observation Plots*

Year	*Per cent. of station average*	*Per cent. of observation plots*
1949	127	..
1950	130	..
1951	114	..
1952	75	133
1953	57	104
1954	53	78

Groundnuts.—On the Station, as in the district generally, wild pig constitute the worst pest of the groundnut crop. Owing to the extensive area of bush, both in and around the Station, efforts to reduce their numbers are difficult and have met with little success. Unhappily they have few natural enemies and are rarely hunted by the meat-hungry Azande, to the majority of whom their flesh is taboo. Although much effort is expended in the protection of crops both by guards and fencing, some damage has occurred in most years to experimental plots at the Station. Yield data for damaged plots have thus been discarded.

Groundnuts showed a marked drop in productivity in the fourth year of cultivation; an average of 505 r.p.f. unshelled nuts for that year, for the six-year-cropping treatment compared with a Station average of 1,200 r.p.f. for groundnuts grown on untreated first- and second-year land. In 1953, the fifth year of cropping, there was a further pronounced drop in yields to 186 r.p.f., as compared with a 1,200 r.p.f. Station average.

In the sixth year of cropping the stand of groundnuts was poor from the outset, representing 48 per cent. of a full stand before and 68 per cent. after resowing, whereas stands of the order of 95 per cent. were obtained elsewhere on the Station with the same seed supply. Later the crop also suffered severely from the depredations of wild pig and rodents, as well as from rosette disease; and what would in any case have been a very small crop now became a negligible one.

Eleusine.—As with groundnuts, eleusine yields showed a marked decline in the fourth year of cultivation. For the six-year-cropping treatment, the average yield of 397 r.p.f. grain in the fourth year compared

with an average of 1,167 r.p.f. per annum for the first three years of the trial and a Station average of 1,040 r.p.f. in that year. The following year the average yield of eleusine plots was only 21 per cent. of the Station average of 1,195 r.p.f. for first- and second-year land. In 1954, the sixth year of cropping, an effective stand of eleusine could not be obtained despite resowing. Growth was bad, heads were small, and a yield of 12 r.p.f. could be written off as negligible.

All three crops under review have shown a drop in level of yield in the fourth year of cultivation. This was most pronounced with groundnuts and eleusine. With cotton, although plants in the fifth and sixth year of cropping were stunted and yields much reduced, productivity was still fairly good and exceeded the average yield for Zande district, where a low level of productivity truly reflected a low standard of crop husbandry.

A cropping-to-exhaustion plot was commenced at the Station in 1951 on a rotation of groundnuts, eleusine, cotton, both phases being present each year [3]. It was sited on a dark loamy soil overlying the usual pea-iron gravel horizon above a red-brown clay. In 1954 the plot was in the fourth year of cropping. Groundnuts and eleusine showed a very considerable decrease in yield after two years of cultivation but the level of cotton yields has been maintained.

These results are in conformity with those of local practice, in which the land is not normally cultivated for more than two to three years running. Nevertheless, the conclusion seems warranted that with farm standards of cultivation land could be cropped effectively for as much as three years.

Soil Characteristics and Nutrient Status

The main characteristics of the agricultural soils of this area, of which the experimental blocks were representative, may be summarized thus:

(*a*) Formed *in situ* and often on the slope.
(*b*) Generally free-draining and leached.
(*c*) Profile dominated by the presence of varying amounts of pea-iron gravel.
(*d*) Acid, pH usually ranging from 5·0 to 7·0.
(*e*) Good crumb structure in virgin soil.
(*f*) Roots penetrate freely to considerable depth.
(*g*) Low humic status; consequently the water-retentive capacity is low.
(*h*) Numerous termite channels.
(*i*) Clay content variable; from 10–30 per cent. in top soil.
(*j*) Principal clay mineral has been shown to be kaolinite.[1]
(*k*) Nitrogen status below 0·2 per cent. in the top soil with an abrupt fall in succeeding horizons.
(*l*) C/N ratios frequently of the order of 12 for top soil.
(*m*) Exchangeable calcium low, of the order of 2–6 milliequivalents per cent.

[1] Unpublished data.

(*n*) Hardpans are infrequent apart from the occurrence of 'mungas'. (Lateritic outcrops with characteristic mushroom-shaped termiteria and distinctive grasses.)

In order to study the possible effect of the different treatments on the soil-nutrient status, a number of blocks were selected for more detailed examination. The difficulties of obtaining the requisite analytical data on a sufficient scale were realized as well as the inherent errors present in the most careful field sampling.

Four blocks, viz. Nos. 3, 11, 15, and 18, were selected for sampling and analysis, which was carried out at the beginning of the trial in 1949 and at its conclusion in 1955.

Crop yields for the four- and six-year-cropping treatments on these four selected blocks followed the same general trend as for the overall average yields. Thus eleusine yields were negligible in the sixth year of cropping; for groundnuts a poor stand in the sixth year was followed by severe rosette disease and pest damage. With the exception of Block 3 (one of the least productive of the trial) the level of cotton yields was fair after six years' cropping. In the fourth year of cultivation, cotton being the sixth crop after opening, yields of over 1,000 r.p.f. seed cotton were still obtained in Blocks 15 and 18 in a good season. It is noteworthy that a high level of yields was obtained in Block 15 despite a high pea-iron-gravel content and the fact that surface outcrops of laterite occurred.

TABLE 5. *Levels at which Soil-profile Pits were Dug*

	Metres
Gallery forest floor	0
Block 25	11
Block 18	22
Summit of hill	23
Block 15	22
Block 11	18
Block 3	16

A series of soil pits was first dug, one at the corner of each of these four blocks, in December 1949 and sampled. The line of pits was surveyed and the levels are shown in Table 5.

Brief field notes of the profiles of the four selected blocks are given below:

Block 3

0–20 cm.	Dark grey-brown, sandy soil with pea-iron gravel. Some crumb structure. Humic and friable. Numerous live roots, fine and coarse.
20–75 cm.	Passing gradually into the B horizon. Red-brown, compact pea-iron-gravel zone. Some iron-stained quartz. Red-brown clay towards the bottom of the horizon. Fine roots throughout.
75–180 cm.	Red-brown clay with little pea-iron gravel. Buff and yellow mottling in lower half of the horizon. A few fine roots.

Block 11

0–8 cm.	Blackish brown, friable, sandy loam. No pea-iron gravel. Numerous live roots.

8–200 cm.	Red-brown, sandy clay loam with some pea-iron gravel at the bottom of the horizon. Live roots throughout.
200–300 cm.	Red clay with yellow mottling. Very hard. No roots. Occasional quartz fragments.

Block 15

0–28 cm.	Dark brown, sandy soil with pea-iron gravel. Numerous coarse roots.
28–130 cm.	Red-brown, pea-iron-gravel horizon. Hard at the top; progressively softer with depth. Moister, redder, more clay and less pea-iron gravel with increasing depth.
130–180 cm.	Red-brown, moist clay with very little pea-iron gravel. Occasional fine roots.

Block 18

0–22 cm.	Dark brown, sandy clay with occasional pea-iron gravel. Humic and friable. Numerous live roots, fine and coarse.
22–125 cm.	Red-brown sandy clay. Much pea-iron gravel at the top of the horizon decreasing with depth. Fairly hard consistency at the top, progressively softer with depth. Some coarse and fine roots throughout. Weathering rock fragments.
125–210 cm.	Red-brown, hard, sandy clay with yellow flecks. Little pea-iron gravel. Occasional roots and weathering rock fragments.

These profiles were sampled in December 1949 in two steps of 15 cm. each and then by 30 cm. steps down to 180 cm. The final samples of the top soil were taken from each of the duration-of-cultivation treatments in each of the four selected blocks in February 1955. Three samples to 15 cm. depth were taken from each of the three plots of each duration-of-cultivation treatment and bulked. A summary of the analytical results is given in Tables 6 and 7.

In Blocks 3 and 11 there was a marked fall in total nitrogen with increasing periods of cultivation, and Block 18 showed the same tendency though less clearly. Block 15 gave contrary results. Here the profile shallowed towards Block 14 and, on the margin of the block, hard laterite was found outcropping with lumps of laterite rock present in the soil. It is noteworthy that in 1949 a figure of 0·22 per cent. total nitrogen and of 2·6 per cent. organic carbon had been found for the surface soil above hard laterite in Block 14. There is perhaps some evidence that restricted profiles in lateritic areas tend to exhibit soils of higher nutrient status than do deeper profiles (cf. Jewitt [4]), which might account for the general higher level of crop productivity in this block. The problem is clearly one for further investigation.

The C/N ratios, all of which came within the range of 10·4 to 14·6, bore no apparent relationship to length of cultivation on these blocks. The correlation between the total nitrogen figures and those for exchangeable calcium was significant (Correlation coefficient = +0·8126), a relationship previously noted by Jewitt (*loc. cit.*). Comparison of the percentage of total nitrogen in the top soil, in the samples taken in 1949 and in 1955, showed no striking or consistent differences. But the extreme variability of the stones-and-gravel fraction within the blocks, as shown in Table 7, is remarkable.

TABLE 6. *Soil Analyses of Samples from Four Profile-pits*

Block	*Cm. from surface*	*Stones+ gravel per cent.*	*Per cent. of Fine soil*				*pH (Potentiometric)*	*Total nitrogen (N) p.p.m.*	*Organic carbon (C) per cent.*	*C/N ratio*
			Coarse sand	*Fine sand*	*Silt*	*Clay*				
3	0–15	27	11	47	11	31	6·2	1,656	2·86	17·3
	15–30	71	10	50	10	30	6·0	1,135	1·78	15·7
	30–60	81	15	40	10	35	6·1	719	0·92	12·8
	60–90	70	13	27	7	53	5·9	553	0·51	9·2
	90–120	62	10	26	5	59	5·8	473	0·41	8·7
	120–150	18	7	29	6	58	5·9	265	0·22	8·3
	150–180	7	7	26	11	56	5·9	102	0·16	15·7
11	0–15	1	21	42	6	31	6·2	1,003	1·45	14·5
	15–30	1	21	38	5	36	5·8	669	0·80	12·0
	30–60	3	21	30	5	44	5·8	506	0·49	9·7
	60–90	0	19	32	6	43	6·0	378	0·34	9·0
	90–120	2	17	33	4	46	6·1	376	0·34	9·0
	120–150	11	20	29	1	50	6·3	324	0·29	9·0
	150–180	14	18	28	5	49	5·2	271	0·27	10·0
15	0–15	22	18	45	8	29	6·6	1,304	1·63	12·5
	15–30	69	25	38	9	28	5·8	561	1·24	22·1
	30–60	75	28	28	12	32	5·1	580	0·64	11·0
	60–90	69	19	26	7	48	5·3	450	0·46	10·2
	90–120	66	15	21	6	58	5·6	399	0·39	9·8
	120–150	60	15	18	7	60	5·5	327	0·31	9·5
	150–180	36	14	20	3	63	5·4	246	0·25	10·2
18	0–15	5	21	52	3	24	6·1	759	0·95	12·5
	15–30	48	21	46	6	27	5·3	557	0·91	16·3
	30–60	47	19	41	8	32	5·1	385	0·55	14·3
	60–90	53	19	34	6	41	5·1	369	0·31	8·4
	90–120	20	15	35	6	44	4·9	325	0·26	8·0
	120–150	15	14	32	9	45	4·9	255	0·22	8·6
	150–180	32	13	32	6	49	4·9	156	0·19	12·2

TABLE 7. *Analyses of Top Soil After Six Years of Treatment*

Block	*No. of years under cultivation*	*Colour (Munsell Number)*	*Stones+ gravel per cent.*	*Per cent. of fine soil*				*pH (Glass electrode)*	*Total nitrogen (N) p.p.m.*	*Organic carbon (C) per cent.*	*C/N ratio*	*Exchangeable Ca. m.e. per cent.*
				Coarse sand	*Fine sand*	*Silt*	*Clay*					
3	Nil	2/2	17	13	51	16	20	6·8	1,374	1·59	11·6	5·8
	First 2	3/2	31	22	50	13	15	6·5	1,282	1·66	12·9	5·8
	First 4	3/4	58	16	54	8	22	6·5	1,125	1·51	13·4	4·9
	All 6	3/4	32	19	52	10	19	6·3	1,016	1·48	14·6	4·5
11	Nil	4/3	14	31	41	9	19	6·8	1,245	1·44	11·6	5·7
	First 2	3/3	4	20	47	14	19	6·8	1,003	1·23	12·3	5·2
	First 4	4/3	4	23	48	11	18	6·7	915	1·21	13·3	4·5
	All 6	3/3	3	27	52	6	15	6·7	920	1·11	12·1	4·4
15	Nil	2/2	30	16	52	22	10	6·6	1,205	1·64	13·6	4·2
	First 2	2/2	10	19	52	15	14	6·7	1,341	1·40	10·4	5·8
	First 4	2/2	31	12	57	11	20	6·6	1,367	1·64	12·0	5·3
	All 6	2/2	41	22	53	12	13	6·7	1,640	1·74	10·6	5·8
18	Nil	3/2	23	23	47	6	24	6·5	941	1·04	11·1	3·1
	First 2	3/2	23	28	51	7	14	6·3	874	1·09	12·5	3·1
	First 4	3/2	27	23	48	6	23	6·2	927	1·09	11·8	4·0
	All 6	3/2	39	29	47	7	17	6·2	814	0·95	11·7	2·7

The progressive decline in yields of groundnuts and eleusine in these trials, after the third year, to the point of practical crop failure in the sixth year, is a clear vindication of the local practice of bush fallowing after the second or third year, in the absence of soil-fertility regenerative treatments. Presumably this is the result of exhaustion of plant nutrients from the soil, but the soil analyses here reported strongly discount the possibility that exhaustion of available nitrogen is the prime cause of such crop failure. Further investigation is obviously desirable, with special reference, it is suggested, in the first instance, to possible phosphate or potash exhaustion.

Fallow Regeneration

The study included analyses of vegetation regeneration after cropping. Analyses were made annually of the regenerating vegetation of all fallow plots in the selected blocks for the duration of the trial. The data for Block 18 are summarized in Table 8, only the more important species being recorded. Data are presented for three end plots, which were allowed to revert to natural vegetation immediately after being cleared and burned in 1949, and for three plots each of the two- and four-year-cropping treatments, i.e. a total area $37{\cdot}5 \times 12{\cdot}5$ metres in each case. It was considered justified to pool the data for the three plots of each strip of each duration of cropping treatment since there was no apparent difference in the regeneration of vegetation on plots cropped under the different rotations A, B, and C.

Where practicable the number of individual plants was recorded. Otherwise frequency symbols were used: r, rare; o, occasional; f, frequent; a, abundant; d, dominant; ld, locally dominant, and different combinations of these symbols. Height in feet is recorded in parentheses.

In 1949, prior to opening the land, the area on which the blocks were laid out was typical Combretaceous grass woodland, obviously subject to burning prior to the establishment of the Station in 1947, with areas of dense shrub growth and no tall grass. Block 25 merged into closed Transition Woodland of Anogeissus and Terminalia, characteristic of the vegetation usually found along the edge of gallery forest.

Sections $12{\cdot}5 \times 50$ metres within the blocks, at the site of the four soil-profile pits, were described botanically in 1949. In Block 18 Rottboellia and Beckeropsis were dominant and co-dominant in the grass layer with Imperata locally abundant. Tree and shrub species were those listed in the vegetation analyses carried out during regeneration (Table 8). The scandent shrubs, *Phyllanthus muellerianus* and *Harrisonia abyssinica* together with *Ficus vallis-choudae*, *Securinega virosa*, and *Vernonia amygdalina* were locally frequent.

Recolonization of fallows by vegetation followed the same general trend throughout the trial.

On land which reverted to natural vegetation without any cropping, tall grasses and Imperata were dominant for the first two years, shrub and tree growth made rapid ratoon growth and shrubs became dominant in the third and fourth years. The tall grasses were gradually suppressed

except at the edges of plots and the characteristic grass became *Setaria chevalieri*. Tree growth gradually emerged from the shrub layer.

After six years regeneration plots had a dense shrub cover with emergent trees. Tall grass and Imperata were rare; there was a ground cover of leaf litter with little herb growth. Climbers, *Cissus* spp. and *Mucuna pruriens*, were abundant throughout.

TABLE 8. *Occurrence of More Important Species in Fallows, Block 18*

Date	*January 1951*	*January 1955*		
Length cultivation (years)	0	0	2	4
Length fallow (years)	2	6	4	2
Species				
Grasses				
Imperata cylindrica	o	r	r	d
Panicum maximum	r	r	r	r
Rottboellia exaltata	d	..	r	r
Beckeropsis uniseta	f, ld	r	r	r
Setaria chevalieri	o, ld	r	..	..
Under-shrub				
Desmodium lasiocarpum	r (to 7)	r (to 7)	o (to 5)	o, la (to 8)
Scandent shrubs				
Phyllanthus muellerianus	7 (5–10)	10 (9–20)	6 (4–10)	1 (6)
Harrisonia abyssinica	2 (10)	6 (4–15)	1 (7)	2 (5–8)
Shrubs				
Securinega virosa	o, lf (to 12)	f (to 20)	o (to 9)	r (to 6)
Vernonia amygdalina	r (to 9)	o (to 20)	r (to 11)	..
Ficus vallis-choudae	o (to 9)	o, ld (to 11)	r (to 10)	o (to 6)
Small trees				
Annona senegalensis	4 (6–10)	4 (10–13)	7 (8–11)	1 (7)
Grewia mollis	7 (8–13)	7 (12–15)	5 (8–14)	1 (8)
Bridelia micrantha	6 (3–9)	5 (7–20)	5 (6–11)	2 (4–9)
Piliostigma reticulatum	3 (4–7)	8 (7–17)	7 (4–16)	6 (4–9)
Lonchocarpus laxiflorus	2 (4–7)	2 (5–7)	1 (4)	1 (4)
Nauclea latifolia	3 (5–9)	3 (8–15)	7 (5–12)	2 (3–7)
Trees				
Combretum binderianum	1 (10)	3 (7–17)	4 (5–9)	2 (9)
Combretum ghasalense	8 (4–9)	10 (3–11)	2 (9)	1 (5)
Terminalia glaucescens	19 (4–15)	21 (10–25)	12 (10–20)	3 (8)
Anogeissus schimperi	12 (4–10)	17 (10–18)	10 (16–20)	1 (7)
Vitex cuneata	1 (6)	1 (14)	2 (5–6)	3 (3–7)
Acacia campylacantha	1 (13)	1 (25)	1 (15)	..
Albizzia zygia	12 (4–11)	18 (4–23)	3 (7–12)	..
Phillanthus discoideus	9 (5–11)	7 (20–27)	..	1 (7)
Stereosperumum kunthianum	2 (7)	5 (10–14)	7 (1–14)	1 (4)
Ficus sp. SGH. No. 2143	4 (8–11)	4 (3–19)	11 (10–15)	4 (6–8)

After two years' cropping bush regrowth followed the same pattern and by January 1955, after four years' fallow, tall grass growth had been suppressed in most plots of the trial. Imperata remained locally dominant on a few plots.

Imperata cylindrica is regarded as an indicator of over-cultivated land or land subject to frequent late burning. Preliminary work at this Station has indicated that in Imperata-dominant grass woodland nitrogen is the major limiting factor in crop production and remarkable responses have

been obtained to nitrogen applied to cotton grown on this type of land [3].

In the four-year-cropping treatment, after two years fallows were dominated by Imperata, without exception, and with ratoon shrub and tree growth coming away slowly.

In January 1955, after six years of cultivation, soil coverage was low with *Bidens pilosa* and *Eragrostis* spp. dominant. With the onset of the rains Imperata quickly established itself and was dominant on all plots. After four years' cropping, and more so after six years, a high proportion of the stumps have been killed and the re-establishment of woody species will be slow.

Acknowledgements.—We are indebted to Mr. P. de Schlippe, who was associated with the inception of the trial, since considerably modified; to Mr. T. A. Jones for the analysis of soil samples taken from the four profiles in 1949, and to Dr. E. W. Russell for much valuable criticism.

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THE ECOLOGICAL REGIONS OF KENYA: THEIR CLASSIFICATION IN RELATION TO AGRICULTURAL DEVELOPMENT

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With PLATES 1–6

Summary

In this paper the writer seeks to present an approach to the problems of development based upon ecological classification. Kenya consists of regions with strongly contrasted environment, and these extend widely into neighbouring territories. Such regions are clearly defined by major plant communities. The communities are described and an account is given of their reactions to present forms of utilization. The main implications of the approach are outlined, in order to indicate the necessity for the classification as a basis for investigation and its desirability as a means to induce better co-ordination of biological research throughout an extensive region of tropical Africa.

A STRIKING feature of the East African environment, particularly that of Kenya, is the existence of regions of strongly contrasted conditions, clearly defined by dissimilar types of vegetation. The marked differences of climate are induced by elevation and aspect of the land. In general, this part of Africa to the east of the Uganda border consists of a vast region of plains supporting semi-desert vegetation, with the main elevated mass of the Kenya highlands lying to the south-west. The semi-desert region extends to the north-east and east through the neighbouring Somaliland territories, but there are scattered outliers of the highland region, which itself may be regarded as an extension of the great highland mass of Abyssinia in the north. The powerful effect exerted by wide differences of environment upon the distribution of wild and domestic animals and upon the activities of man is clearly evident. In fact, the whole region affords exceptional opportunity for study of the reactions of various forms of life to rapid changes of environment from one area to another. The present account of the vegetation is an elaboration, in the light of further knowledge accumulated, of the information presented in the *Journal of Ecology*, 1940, volume xxviii, pages 377–85, under the title 'A Vegetation Map of Kenya, with particular reference to grassland types'.

Climatic Conditions

Kenya is situated on the equator, extending approximately 4½ degrees north and south of it, and lying between 34 and 42 degrees east. Its land area is 219,730 square miles. Six main ecological regions, defined by major plant communities, have been recognized. The communities occur, in each case, as several isolated masses together with numerous minor aggregates, and they extend into the adjoining territories, particularly to the north-east and south. Relatively moist vegetation types

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occupy the south-western quarter of the country which consists mainly of the highland mass and includes the Lake Victoria basin to the west. The remainder, with the exception of a somewhat moist tropical belt at the coast, supports only semi-desert bush and scrub.

The climatic factor of greatest significance in East Africa is moisture which, together with temperature, is responsible for the existence of distinctly different major plant communities. Meteorological data are very incomplete, particularly in the sparsely populated, extensive dry regions, but as a rough guide it may be stated that the arid conditions of the north and east of Kenya, and the Somaliland territories beyond, represent an erratic annual rainfall of approximately from 10 to 15 inches. Parts of this dry region, such as the neighbourhood of Lake Rudolf, receive no more than 5 inches of rain. To the west of Kenya, near Lake Victoria, high rainfall occurs, varying from 60 to 80 inches in different localities. The rain is derived from the south-east and north-east monsoons, which blow from the Indian Ocean from April to June and again in November. The monsoon is intercepted by the south-western mass of elevated land, which causes a relatively sharp break towards high-moisture conditions. In addition, the climate of that part of Kenya to the west of the Great Rift valley, which cuts through the country roughly north and south, is influenced by rain-bearing winds from Lake Victoria, which result in precipitation during the months of July and August. The elevated mass of the highland region extends from 3,800 feet at the lake, and includes peaks such as Mount Kenya (17,040 feet), the most extensive part of the region being at about 6,000 feet or a little below. In comparison, the lower plains, which support vegetation adapted to extremely dry conditions, lie mainly between 1,000 and 2,000 feet. The climate of the highland region is characterized by relatively high moisture and low temperature over considerable parts of the area [1]. In addition to rainfall, mists constitute an important factor, both at the higher altitudes and in the coastal belt, where they appear to exert considerable influence upon the vegetation of these localities.

Rainfall records alone provide a very inadequate guide to the prevailing conditions, and even these records are sparse, while evaporation, for which few data are available, is of great importance throughout, particularly so in the wide region of semi-desert vegetation. Temperature is always sufficiently high to permit of biological processes, given sufficient moisture, and it is the latter which is frequently the determining factor where vegetation is concerned. Between certain of the major units under similar total rainfall, however, temperature appears to be the ruling factor. This is notably the case in determining the boundary between the Highland Grassland and the Combretum—Hyparrhenia Scattered-Tree Grassland (see description of communities and photographs). In attempting to assess the relative importance of moisture and temperature in this region of the tropics, it is well to appreciate that, unlike the temperate zones, it is always low moisture and not low temperature which is liable to inhibit plant growth.

Various attempts have been made to classify world climate with a view to defining regions of known conditions, none of which can be

successfully applied to East Africa. Lack of sufficient data on rainfall (particularly its distribution in time) and evaporation makes impossible any such effective classification [2, 3].

TABLE 1. *Selected Meteorological Records*

Station	*Plant community*	*Altitude ft.*	*Mean annual rainfall in.*	*Mean annual temps.*		*Mean annual evaporation mm.*
				Max. °F.	*Min. °F.*	
Eldoret	Highland Grassland and Forest (transitional)	7,050	40·11	75·9	49·0	921
Kisumu	Scattered-Tree Grassland: Combretum—Hyparrhenia	3,760	47·80	84·9	63·0	1,236
Mombasa	Coastal High-Grass—Bush	53	47·33	86·1	74·1	794
Naivasha	Scattered-Tree Grassland: Acacia—Themeda	6,234	23·15	77·4	49·4	1,358
Mandera	Desert Scrub	1,085	8·25	93·1	75·5	2,421
Kericho	Highland Grassland and Forest	6,500	71·49	78·8	49·0	..
Kitale	Scattered-Tree Grassland: Combretum—Hyparrhenia	6,220	44·92	77·5	53·7	..
Nanyuki	Scattered-Tree Grassland: Acacia—Themeda	6,389	26·74	74·6	48·1	..

Note. The stations with evaporation figures do not well represent the plant communities because the selection is determined by the few evaporation data published. These values are obtained by multiplying by 0·5 the readings from Piché Evaporimeters and they are said to approximate to evaporation from a free-water surface. Three stations more representative of communities have been added without these figures but the present distribution of meteorological records does not permit of a satisfactory selection.

To summarize the climatic conditions of Kenya very briefly, the greater part of the country to the north and east is arid and hot, while towards the west there is a tendency for change to the moist tropical conditions of the adjoining territory of Uganda. The highland mass intervenes in the central and south-western part of the country, with a climate (including wide variations) which may be generally described as sub-tropical, except with regard to the short day-length connected with its geographical position on the equator.

The Plant Communities

In the past, provision for comprehensive ecological survey of the East African territories, comprising Kenya, Uganda, and Tanganyika, has not been available and knowledge of the vegetation and soils tends to be localized and poorly co-ordinated. An interterritorial pasture research conference convened in 1940 [4] emphasized the necessity for such provision, but the demands of the war period prevented the recommendations from being implemented. The project has now become the responsibility of the East African Agriculture and Forestry Research Organization, established under the East Africa High Commission in 1947, and charged with co-ordination of research in the territories.

The only attempted classification of vegetation which covers these three countries is that incidental to Shantz's description of the vegetation of the continent [5]. This pioneer work, while providing a valuable perspective, is inadequate in the light of recent knowledge. Contributions to the knowledge of classification in Tanganyika were made by Engler [6], when the territory was German East Africa, Phillips [7], and Burtt [8], while in 1949 Gillman compiled a 'vegetation-types map' of that country [9]. Subsequent to Shantz's generalized account in 1923, no attempt was made to classify the vegetation and indicate the distribution of the communities in the other two territories, Kenya and Uganda, until the work undertaken by the writer in respect of Kenya, which resulted in the publication of two maps [10, 11]. The major plant communities, according to the classification adopted in the second of these maps, were described in two further publications [12, 13].

The terminology employed in the description of African vegetation is in need of consideration on a broad basis, since at the present time there is insufficient agreement even between workers in different territories under the same national administration. It is important that this matter should receive early attention, in view of the fact that knowledge derived from ecological survey constitutes an essential basis for development in these regions, where political advance threatens to outstrip progress towards correct land usage. The names given to the communities in the present classification are based upon those used by Shantz, but they have been adapted so as better to describe the vegetation according to present knowledge. Also, an attempt was made to conform in some degree to the views of specialists at the 1940 East African conference mentioned above, and this resulted in the acceptance, amongst other terms, of the name 'Scattered-Tree Grassland' in place of 'Savannah' to describe grassland through which trees are distributed. In addition, however, a sub-title indicating the dominants is used for some of the communities and this improvement could well be extended to the others, when the sub-division which appears desirable in some cases leads to more precise knowledge of their composition. The findings of the conference on terminology did not reach finality, and although the names used for the major units of vegetation in the present classification are not regarded as entirely satisfactory by the writer, their improvement should await discussion representative of wide regions of the continent, as already indicated.

The description deals with the main units of vegetation shown on the accompanying map (Fig. 1); the formation in the sense defined by Clements [14]. Reference is made to some of the more important associations determined by soil type which occur within these major units, but in most cases the associations cannot be shown and their definition on larger-scale maps is a further step which must be taken towards providing knowledge which bears closely upon the problems of development. Special significance is attached to the type photographs of plant communities which are important to the description.

The six main vegetational units of Kenya, in descending order of the moisture conditions which they appear to represent, are as follows:

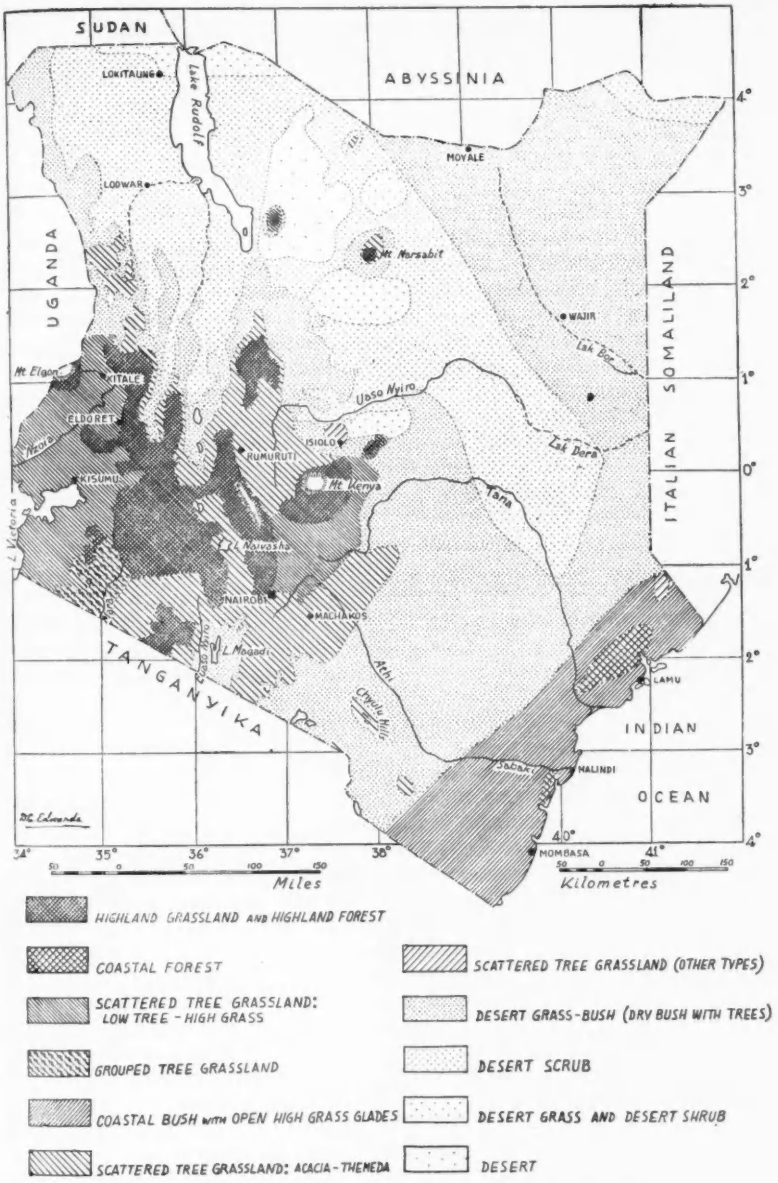

FIG. 1. Vegetation of Kenya. The major plant communities

This map was first published in *Important Grassland Plants of Kenya*, Edwards and Bogdan, 1951. Sir Isaac Pitman and Sons Ltd., London.

1. Highland Grassland and Forest.
2. Scattered-Tree Grassland: Low Tree—High Grass, or Combretum—Hyparrhenia.
3. Coastal High Grass—Bush.
4. Scattered-Tree Grassland and Open Grassland: Acacia—Themeda.
5. Desert Grass—Bush (Dry Bush with Trees): Commiphora—Acacia—Desert Grass.
6. Desert Scrub.

The plant communities which define the main ecological regions are dependent primarily upon climate, but so much has yet to be learned of the climatic factors involved in the whole region under discussion, that no more than a rough guide can be given in the form of average annual rainfall and altitude range. It may be noted, however, that in general, the lower the rainfall the more erratic it tends to be. In the present state of our knowledge, the first and most important step towards correct development is definition of the ecological regions by means of the existing vegetation. The determination of the factors composing the environmental complex represented by each community will provide an important field of future research.

Highland Grassland and Forest. Figs. 2 and 3. This vegetation occurs in the highlands of Kenya, and is of limited extent. It is situated on isolated masses of elevated land, chiefly between 6,500 and 9,000 feet, with annual rainfall, mainly from 40 to 50 inches, varying between 35 inches (at the drier transitional fringe) and 90 inches on some of the eastern slopes of forest. The moisture conditions throughout are supplemented by mountain mists. Both relatively low temperatures and high moisture determine the distribution of the community. The prevalent soil type is a deep lateritic loam derived from a porous lava rock, locally known as Kikuyu Red Loam.

The community consists mainly of a patchy distribution of comparatively small areas of forest in extensive areas of undulating, open grassland, with forest tending to occupy the eastern slopes.

In general, a belt of bamboo (*Arundinaria alpina*) is found at the higher and moister fringe of the evergreen forest, extending to about 10,000 feet elevation, while at the lower and drier edge the forest consists largely of cedar (*Juniperus procera*) and olive (*Olea chrysophylla* and *O. hochstetteri*). According to the revision of *Trees and Shrubs of Kenya Colony* [15], the mountain forest falls into two main types related to moisture conditions: (*a*) a high-moisture type under annual rainfall of from 55 to 90 inches, confined mainly to the eastern slopes of the mountain masses; and (*b*) a lower-moisture type subject to rainfall of from 35 to 55 inches. The former is characterized by the absence of cedar and is largely dominated by *Ocotea usambarensis* (East African camphor) and *Podocarpus milanjianus*. The latter is composed chiefly of *Juniperus procera*, *Podocarpus milanjianus* (at higher altitudes), *P. gracilior*, *Olea chrysophylla*, and *O. hochstetteri*.

The rolling grasslands are chiefly dominated by *Themeda triandra* (Red Oat grass) which constitutes a sub-climax dependent upon periodical fire. Wherever grazing is intensified just enough to prevent grass

fires, a useless coarse-grass phase strongly dominated by *Pennisetum schimperi* and, in localized areas, by *Eleusine jaegeri*, takes possession of the land. In the more typical area of the vegetation, where the annual rainfall is above 40 inches, the clearance of forest is followed by herbage composed mainly of stoloniferous *Pennisetum clandestinum* (Kikuyu grass) which is capable of being developed as a productive sward in which the grass is associated with *Trifolium johnstoni*[1] (Kenya White clover). The dominance of Kikuyu grass is favoured by management which maintains short herbage and a high level of soil fertility [16]. In the absence of this factor, the *P. schimperi*-dominated coarse phase intrudes in most parts of the region and eventually replaces the Kikuyu grass herbage.

The typical part of this community, which may be called the potential Kikuyu-grass region, occupies a relatively restricted area situated within the above altitude limits (6,500–9,000 feet), but with minimum annual rainfall of 40 inches. This vegetation is surrounded by a more extensive belt, subject to lower moisture conditions although not necessarily at lower altitudes, transitional between it and the adjoining communities. In the transitional belt Kikuyu grass does not occur naturally as a dominant, and it cannot be economically maintained as the chief constituent of the herbage.

Other grasses of importance in the community are *Andropogon chrysostachyus*, *A. pratensis*, *Exotheca abyssinica*, *Digitaria scalarum*, *Eragrostis lasiantha*, *Setaria sphacelata*, and *Agrostis* spp. These grasses are found in association with *Themeda triandra* in the fire-sub-climax stage and also occupying the ground between the large tufts of *Pennisetum schimperi* in the coarse-grass phase, which latter is particularly true of *Andropogen chrysostachyus* and *Digitaria scalarum*. In the transitional zone, in addition to the two main species of the coarse-grass phase already mentioned and several of the foregoing species, other large-tufted grasses such as *Pennisetum catabasis* and *Sporobolus filipes* are conspicuous in some areas. Reference has already been made to the occurrence of *Trifolium johnstoni* (= *T. semipilosum*) as a natural constituent of Kikuyu-grass herbage in the high-rainfall portion of the community. It also extends throughout the transitional zone, and it tends to appear wherever land is bared by cultivation. Many leguminous herbs (including other clovers) are of minor importance, and one which may be mentioned is a clover with large violet-purplish flowers, confined to the higher elevations between about 8,000 and 9,000 feet. This species probably represents true *T. johnstoni*, Oliv.

Mountain moorland is found beyond the forest line in this region, but for the purpose of the present discussion it is of little practical significance.

Scattered-Tree Grassland: Low Tree—High Grass, or Combretum—Hyparrhenia. Fig. 4. The community to which this name is given consists of grassland with herbage 5 to 8 feet in height, thickly scattered with small trees which are mostly 10 to 15 feet high. The appearance

[1] Recent taxonomic work at the Royal Botanic Gardens, Kew, suggests that this species might be more correctly known as *Trifolium semipilosum*, Fresen., var. *glabrescens*, Gillett var. nov.

of the vegetation is often reminiscent of a cultivated orchard. Larger trees about 30 feet high are distributed in some areas, and a characteristic feature of wide regions is the existence of isolated small areas of taller forest trees (50 to 90 feet), evidently resulting from exceptional ground-water conditions. This vegetation type covers an extensive area. It occurs in two main masses; in the Lake Victoria basin to the west, and to the south and east of Mount Kenya. It also extends into the adjoining territories of both Uganda and Tanganyika. The community is found mainly between 3,000 and 6,000 feet, and the annual rainfall is estimated to vary from one part to another between 35 and 60 inches. The vegetation described may also be regarded as a fire sub-climax. It is evidently related to forest and is maintained in its present stage by the frequent passage of fire. In the absence of this factor thicket tends to replace the high grass between the scattered trees.

Typically, the small trees of this vegetation are broad-leaved and deciduous with characteristic fissured corky bark. The most general dominant is *Combretum splendens*, while other important trees are *Erythrina tomentosa* and species of Terminalia, Ficus, Faurea, Heeria, Dombeya, and Bauhinia. The grasses which contribute mainly to the 'high-grass' character of the community are members of the genera Hyparrhenia and Cymbopogon. *H. rufa* is the most important of the former, and of the latter *C. afronardus* in the western mass of the vegetation and *C. validus* in the area about Mount Kenya. The herbage is, however, often complex with a considerable range of grasses. Some of the more common of these are *Themeda triandra* (dominant in localized areas), *Panicum maximum*, *Setaria sphacelata*, *Sporobolus pyramidalis*, *Brachiaria brizantha*, *B. soluta*, *Chloris gayana*, *Setaria* spp., *Loudetia kagerensis* (localized dominant), *Digitaria gazensis*, *Beckeropsis uniseta*, *Paspalum scrobiculatum* var. *commersonii*, and *Cynodon dactylon*. Legumes are not abundant, but some of those which appear to be significant from the pasture standpoint are species of Crotalaria, Astragalus, and Dolichos, together with *Glycine javanica* and two annual clovers, *Trifolium steudneri* and *T. subrotundum* (= *T. rueppellianum*), these last two occurring in moist situations.

The soils of the main region of the community are freely drained and often of a somewhat sandy nature, but adjoining this vegetation is a comparatively limited region in the Trans-Mara and Sotik districts of Kenya where impeded drainage induces a sub-type of the main Combretum—Hyparrhenia community. This has been called the 'Grouped-Tree Grassland' (Fig. 5), and it consists of distinct groups of trees and bushes separated by areas of strongly tufted coarse grasses, the whole presenting the appearance of a vast parkland. This vegetation is situated within the altitude and rainfall limits of the main community (at about 6,000 feet and 50 inches), and the cause of the seasonal water-logging is evidently the peculiar soil which contains a hard pan slightly below the surface, underlain by a deep layer of grey clay. The tree groups are confined to the sites of old termite hills, which are raised above the level of the surrounding land and therefore escape the swampy conditions which prevail intermittently.

The trees which form the characteristic, isolated groups are from 20 to 50 feet high. They consist of some of the more common species mentioned above, together with such species as *Olea chrysophylla*, *Rhus glaucescens*, *Teclea nobilis*, *Pittosporum abyssinicum*, *Hippocratea* sp., *Acokanthera friesiorum*, and *Carissa edulis*. Over considerable areas within this sub-type the herbage is dominated by *Themeda triandra* and it is subject to periodical fire, but in the seasonal swamps which constitute the most characteristic feature of the vegetation the ground between the tree groups is thickly occupied by large tufts of *Pennisetum catabasis* or of a large species of Andropogon. Between the tufts and intermingled with the large grasses occur somewhat finer ones, such as *Hyparrhenia ruprechtii*, *Sporobolus pyramidalis*, and *Loudetia kagerensis*, which last also dominates localized areas of the region.

Coastal High Grass—Bush. Figs. 6 and 7. A relatively narrow coastal belt of Kenya is occupied by tropical vegetation of a somewhat dry nature when compared with the rain forest of tropical regions towards the west of central Africa. Furthermore, this belt of moist vegetation ceases slightly north of the frontier with Italian Somaliland, where it merges into semi-desert vegetation. The annual rainfall of the coastal strip proper varies approximately from 38 to 50 inches and altitudes are in the main less than 1,000 feet. The climate is, however, distinctly humid at certain times of the year, and the moisture conditions cannot be truly appreciated from a consideration of the rainfall figures alone. A mist belt is defined by the prevalence of lichen on the bushes and trees, often extending to a considerable distance inland from the coast.

Vegetation subject to these moisture conditions occurs as a coastal strip usually not over ten or fifteen miles wide, beyond which, with rapidly decreasing moisture, a transitional region extends to the desert vegetation lying farther inland. In the whole of this region, including the coastal strip, the effect of climate in determining the nature and distribution of the vegetation is influenced by the soil types to an unusual degree, chiefly as these soils affect the availability of water. Deep sands with low moisture-retentive powers are prevalent, particularly towards the south, while a widespread type in the transitional region consists of shallow soil underlain at a few inches by shale.

Coastal High Grass—Bush is the name given to the vegetation of the coastal strip, which consists of dense, high bush with limited areas of forest and extensive open glades. In the past, the forest probably occupied much more of the area, but centuries of cultivation during the slave-supported Arab tenure probably reduced the forest considerably in certain parts of the region. On the seaward fringe of this vegetation mangrove swamps occur in tidal estuaries and lagoons, while *Casuarina equisetifolia* and coconut palms are characteristic trees at high-tide line. A narrow zone of Doum palm (Hyphaene) is found near to the coastline. Two species are concerned, *H. coriacea* and *H. parvula* (unbranched). The former, branched palm is the more common, and is found for a considerable distance inland, chiefly scattered in open areas of high grass which are subject to seasonally swampy conditions. One observer

claims that this palm is spreading as a result of its ability to withstand frequent grass fires [17].

The surviving areas of forest vary with soil type, particularly with regard to its effect upon available moisture as noted above, and also with a general trend towards drier conditions to the north. Where the soils consist largely of deep sands in the south, open woodland is dominated by *Brachystegia oliveri* and this tree also forms an important constituent of limited areas of forest confined to ridges in this region of frequent seasonal swamps. In areas of the more favourable moisture conditions, such species as *Afzelia quanzensis* and *Trachylobium verrucosum*, together with many others, are important, while the drier forests towards the north are characterized by *Brachylaena hutchinsii*, *Mimusops sulcata*, *Ficus* spp., *Diospyros* sp., *Dobera roxburghii* (= *D. glabra*), and *Euphorbia* spp.

The vegetation of the main region consists of high bush in which some of the forest species occur mixed with a complex of many bush types. Scattered Baobab trees (*Adansonia digitata*) often present a striking feature, while tall mango trees, resulting from ancient human occupation, are found in localized areas of better soil. A general feature of this vegetation is the existence of open glades, which appear to be primarily due to seasonally water-logged conditions. Such areas are, however, subject to frequent grass fires, and this factor is also in part responsible for checking the advance of the tree species. These open areas are occupied by a rank growth of grass 8 to 10 feet high, the most important species being *Hyparrhenia rufa*, which often forms a practically pure stand. On better-drained land *Pennisetum polystachyon* and *Rottboellia exaltata* form similar tall herbage, particularly towards the south of the region. In areas of recently cleared forest, herbage 6 to 8 feet high is dominated either by *Panicum maximum* or *Digitaria* sp. near *D. macroblephara*, depending upon the locality. With the approach to lower rainfall conditions towards the north, the high-grass character of the vegetation is to some extent lost, and such species as *Eragrostis superba*, *Cenchrus ciliaris*, and *Chloris myriostachya* assume greater importance in the herbage. These grasses are widely distributed throughout the coastal region, but in the comparatively open woodland of the northern areas *C. myriostachya*, which is a dominant of the drier inland vegetation, extends into the open glades and, together with a coarse Sporobolus species, frequently dominates these areas.

The relatively narrow strip of vegetation which has been named the Coastal High Grass—Bush is separated from the semi-desert vegetation lying inland by a wider transitional belt, which is at first moderately productive but rapidly approaches in nature the adjoining dry community. The transitional vegetation varies from closely growing bush to open, 'orchard' bush with scattered trees. The chief constituents are Acacia species with Diospyros, Terminalia, and Combretum on the moister side, changing to Commiphora and Acacia farther inland. Candelabra Euphorbia is prominent over considerable areas and Sansevieria is widely distributed. Amongst the small trees *Terminalia prunioides* and *Dobera roxburghii* are often conspicuous, and the bush

Thespesia danis is very characteristic of some areas. The herbage cover, which is somewhat sparse over the greater part of the area, is dominated by such grasses as *Eragrostis superba*, *Digitaria* spp., *Aristida adscensionis* (possibly resulting from over-grazing), and *Heteropogon contortus*, the last-named being particularly characteristic of the shallow soils overlying shale. *Cenchrus ciliaris* is important in parts of the area, and towards the moist coastal strip Sporobolus, Cymbopogon, and Bothriochloa species are found, with colonies of *Themeda triandra*.

Scattered-Tree Grassland and Open Grassland: Acacia—Themeda. Fig. 8. This easily distinguishable community consists typically of flat-topped Acacia trees widely scattered in an even cover of grass, 3 to 4 feet high. The trees are often 50 feet high, but much of the region is scattered with small, thin Acacia plants only 6 to 8 feet high. The latter most frequently consist of *A. drepanolobium* with prominent ant-galls on the spines. Extensive open areas of grassland occur, where Acacia is little in evidence and where it appears only as isolated plants or in small groups. The vegetation type is the most extensive at intermediate elevations in Kenya. It occurs between 4,000 and 6,500 feet. The annual rainfall, which varies from 20 to 30 inches in different localities, is distinctly erratic and droughts are a feature of the climate.

Some of the more common trees are *Acacia hebecladoides*, *A. seyal*, *A. senegal*, *A. stenocarpa*, and *A. subalata*. Other genera occur occasionally, such as Balanites which is often conspicuous towards the drier fringe of the community. In rocky situations large candelabra-like Euphorbia present a striking feature, and in such localities Aloes and other succulents are common. The main grass-dominant, *Themeda triandra*, appears to be associated with moderately high elevations in Kenya, and it does not assume importance below about 4,000 feet. This grass very generally dominates the tall even cover of herbage in the community, although many other species occur and these vary in importance from one locality to another. The more common of these grasses are *Pennisetum mezianum*, *P. massaicum*, *Eragrostis* spp., *Bothriochloa insculpta*, *Hyparrhenia* spp., *Setaria* spp., *Digitaria* spp., *Cenchrus ciliaris*, and occasionally *Chloris gayana* and *C. virgata*. *Aristida adoensis* and *A. adscensionis* are plentiful where the cover has been affected by agencies such as over-grazing. Towards the drier fringe of the community *Pennisetum stramineum* is dominant in localized areas.

Within the Acacia—Themeda community, an economically important, though limited, sub-type occurs. This is the Tarchonanthus—Cynodon association (Fig. 9) which occupies ancient lake beds, chiefly in the Rift valley. It consists of short herbage strongly dominated by *Cynodon plectostachyum* and *C. dactylon* (Star grasses), with densely scattered bushes or small trees of *Tarchonanthus camphoratus*. In the areas from which existing lakes have receded comparatively recently an almost pure stand of Cynodon is found, the Tarchonanthus assuming importance only on the more extensive, older beds. The two Cynodon species (particularly *C. dactylon*) also occur in favourable situations such as stream margins throughout the Acacia—Themeda vegetation. Leguminous constituents are relatively scarce in the whole of this grassland

community and they are chiefly represented by species of Indigofera and Crotalaria.

In the main ecological region two factors exercise an important influence upon the chief constituents of the vegetation; these factors are impeded soil drainage and fire. The former tends to inhibit the growth of trees and appears to be responsible for the wide tracts of open grassland mentioned above, which are devoid of trees or where Acacia is thinly scattered in dwarf form, and where the main soil type is tropical black earth formed under conditions of seasonal flooding. The latter factor (fire) is closely connected with the dominance of Themeda throughout the region, and experimental evidence indicates that the dominance of this grass is maintained by the frequent grass fires which occur in the dry season [18]. Fire also has a marked effect in retarding the advance of tree and bush constituents. It should not be supposed, however, that the activities of man have been entirely responsible for the fire-tolerant nature of this vegetation. Deliberate grass-burning is widely practised by the pastoral tribes of the region and accidental fires also frequently occur owing to the extremely dry herbage in rainless periods, but it is probable that fires are due in some measure to natural causes and the evidence of recent volcanic activity suggests that it might have influenced the earlier development of the vegetation.

The Acacia—Themeda Scattered-Tree Grassland extends into the adjoining territories of Uganda and Tanganyika, and it is extensively represented southwards in the continent.

Desert Grass—Bush (*Dry Bush with Trees*)*: Commiphora—Acacia—Desert Grass.* Figs. 10 and 11. This vegetation is the most extensive type in East Africa. Together with its more extreme form, the Desert Scrub, it occupies at least two-thirds of the area of Kenya, and it forms a vast community extending to the north-east through the adjoining territory of Somalia almost to the Gulf of Aden [11]. The elevation of the main region is from 1,000 to 2,000 feet, and the low and erratic annual rainfall is estimated to vary from 10 to 15 inches. However, droughts of several years' duration may occur, and a feature of the climate is a desiccating wind which blows during the protracted dry seasons. It is noteworthy that the low moisture conditions permit of few permanent streams throughout this region, and that drainage chiefly takes the form of water-courses which are dry except at short periods immediately following rain.

The community consists of an assemblage of mostly deciduous bushes, 10 to 15 feet high, and usually branching from near the ground with few well-defined trunks. Over extensive areas widely scattered trees, 30 to 40 feet high, project through the bush growth, and these are regarded as characteristic of the typical community. In the northern region of Kenya the bushes are spaced approximately from 12 to 30 feet apart. The ground vegetation between the bushes consists of scattered tufts of perennial grasses together with low shrubs, leaving much of the surface exposed. Only for brief periods following rain is this cover improved by a transitory growth of annual herbs. For the greater part of the year

the Desert-Grass—Bush is in a drought-dormant condition, when the bushes are leafless and the tufted grasses dry and brittle.

The characteristic dominants of the bush throughout are Commiphora and Acacia, while the scattered taller trees which occur most frequently are *Delonix elata* and *Acacia spirocarpa*, with the Baobab (*Adansonia digitata*) assuming importance in some areas to the south of the community where transition towards the moister coastal vegetation takes place. Common amongst the low shrubs are species of Sericocomopsis, Barleria, Aerva, Disperma, and Indigofera. In many areas, particularly towards the south, the fibre-yielding succulent, Sansevieria, is grouped at the base of the bushes and occasionally forms dense stands. *Acacia mellifera* is one of the most important bush constituents sharing the dominance with Commiphora. Other common bushes and small trees are a twisted Terminalia, *Balanites* spp., *Boscia coriacea*, and *Salvadora persica*, the last named chiefly on saline soil in the flood area of seasonal streams.

The grasses vary somewhat with the region concerned, but probably the most general dominant is *Chrysopogon aucheri* var. *quinqueplumis*. This species is important throughout the whole vast region of the vegetation type but it does not occupy the position of dominant in all areas, as for instance far to the north of the formation in British Somaliland where, although it remains of importance, two large tuft-grasses, *Aristida kelleri* and *A. papposa*, are the chief dominants. Towards the coastal region of Kenya to the south in slightly less dry parts of the community, *Chloris myriostachya* and *C. transiens* are the most important grasses, the latter being associated with scattered *Dobera roxburghii* trees in the bush vegetation. Other important grasses are *Cenchrus ciliaris*, *Enteropogon macrostachyus*, and species of the genera Aristida, Sporobolus, Tetrapogon, Latipes, and Enneapogon, together with Digitaria in localized areas.

Desert Scrub. Fig. 12. The area covered by this vegetation in Kenya and also in the countries to the north-east is second only to that of the Desert-Grass—Bush. The conditions are distinctly drier, the average annual rainfall probably not exceeding 10 inches over the main region and being only about 5 inches in some parts, such as the neighbourhood of Lake Rudolf.

The community consists of low bushes and stunted trees forming a thin cover in which the bare ground is always conspicuous. The bushes are from 4 to 10 feet high; the leaves are small and inconspicuous, and the whole community is in a drought-dormant condition and leafless except for brief periods following rain. The grasses and other herbs are ephemeral, appearing after rain, and perennial grasses are insignificant. For most of the year the sparse ground vegetation consists mainly of small shrubs. Viewed from a distance, the dominating colour of the landscape in this vegetation is that of the bare ground showing through the thin cover of plants.

The two chief dominants of the scrub, Commiphora and Acacia, are the same as those of the Desert-Grass—Bush and many other plants are common to the two communities. The Desert Scrub might, in fact, be

regarded as a dry form of the Desert-Grass—Bush vegetation except that the scattered taller trees described for the latter type are not found in the Desert Scrub, and the virtual absence of perennial grass is of practical importance. Chiefly on the basis of these two factors the community has been defined on the map.

Within the Desert Scrub vegetation are isolated open areas of Desert Grass and Desert Shrub (Fig. 13), often of considerable extent. In these areas the land surface is frequently strewn with lava rubble, but the type also occurs on red desert sand. The herbage consists of an extremely sparse growth of desert grasses intermixed with small shrubs, which latter occasionally assume dominance. Such areas are usually devoid of trees, and bushes are confined to dry water-courses, but in some localities scattered Acacia-trees occupy the lava ridges. The important grasses are species of Aristida (including *A. papposa*), *Chrysopogon aucheri*, *Tetrapogon spathaceus*, *Latipes senegalensis*, and *Enneapogon cenchroides*. Occasionally a small Blepharis species takes the place of the grasses in localized areas, and unusually heavy rain results in a rapid advance of annuals such as *Aristida adscensionis* and *A. mutabilis*. The low shrubs of this community belong chiefly to the genera already mentioned for the Desert-Grass—Bush.

The foregoing discussion of the major plant communities which have been recognized serves to indicate that the vegetation constitutes the best available key to the clearly contrasted ecological regions which exist. The facilities available have permitted survey mainly of a reconnaissance nature and it is desirable that more detailed work should follow with little delay. As additional knowledge has been accumulated recently, it has become evident that some of the communities should be subdivided. The two regions in which this is most likely to be necessary are those of the Highland Grassland and Forest and also the portion of the extensive Desert-Grass—Bush community approaching the coastal belt. As an example, in part of the latter region to the east of the Tana river, the small tree, *Dobera roxburghii* (= *D. glabra*), replaces Commiphora as a prominent constituent of the bush over a considerable area and the herbage cover is frequently dominated by *Chloris transiens*. This apparently distinct community has been tentatively named Acacia—Dobera Grass—Bush, and it is evidently a somewhat higher-moisture type than the Desert-Grass—Bush proper.

In dealing with the main vegetation types, reference has been made to transitional zones. These are often of considerable extent as in the cases described; in other cases they are very limited, particularly where high scarps are concerned, but there is almost invariably a belt in which the vegetation contains elements belonging to the communities on both sides of it. In general, such zones have been shown on the map as part of the higher-moisture community to which they are related.

Reactions to Utilization in the Various Regions of Vegetation

A consideration of the present forms of land utilization, their effect upon the vegetation and, through the reactions of the plant cover, upon the soils, will quickly lead to an appreciation of the basic problems of

development. These problems are mainly of a conservation nature, concerned as they are with the necessity to correct a downward trend. At the present stage of development in East Africa, difficult sociological problems must be solved before the results of research can be fully translated into practice, but given this advance, it is knowledge concerning the use of grassland which stands foremost in the requirements of progress.

Apart from the limited coastal region where occupation is restricted to certain parts through scarcity of water-supplies and unsuitable soils, the two vegetation types subject to relatively high rainfall (Highland Grassland and Forest, and Combretum—Hyparrhenia Scattered-Tree Grassland) support large native agricultural populations together with separate and less extensive areas of European farming. The native methods of land utilization have developed little with the changed conditions of modern times, and they are still based upon shifting cultivation in which soil recovery is dependent upon a period of bush fallow. In the region of the plant community first-named above, European farming mainly takes the form of extensive ranch properties, and in the other it consists of cash-crop production which has been pursued in the past with little provision for soil recovery.

In the regions of native agricultural occupation a serious problem of soil degradation has arisen, often involving severe erosion. This is a sequel to the advance of European administration and development, which in the comparatively short period of little over fifty years has caused the cessation of inter-tribal warfare and has attained a large measure of control over both human and animal diseases, resulting in a greatly increased population of men and animals. With the removal of the threat of raids, occupation of these higher-rainfall regions has become more stable and agriculture has taken the form of intense food and cash-crop production, but without any essential change in the methods employed to meet the changed conditions. In short, a balance has necessarily been destroyed, which tended in the past to stabilize the human and animal populations, and at the same time the emphasis has been shifted from the primitive requirements of a subsistence economy to that of cash-crop production, as a result of the needs created by contact with civilization. In addition, the increasing pressure of population in the moister regions results in a constant tendency on the part of the agricultural and semi-agricultural tribes to expand into areas which are ecologically incapable of supporting their mode of living without marked detriment to the vegetation and soils [12]. The situation outlined constitutes the most urgent and difficult problem of development in East Africa. Its solution lies in the possibility of deflecting the population surplus to the carrying capacity of the land into channels such as industry (as these can be developed), and in the establishment of improved methods of land utilization. The latter step is rendered the more difficult because of land fragmentation which results from the existing form of inheritance, but it is clearly evident that the future progress of the territories concerned is dependent upon the possibility of introducing in the areas of African occupation methods of farming

which will preserve a balance between utilization and deterioration of the land.

Prior to the development of the situation described above, the bush fallow of shifting cultivation provided a sufficient means of maintaining the soil within the two moist plant communities concerned, but in connexion with the greatly intensified utilization which now exists, the period of fallow has been so reduced (in some cases it has disappeared entirely) that it has become quite inadequate to maintain fertility. The first essential step to check the downward trend is the introduction of utilizable, temporary grass in place of the former bush fallow. The evidence of recent observations and experiments indicates that deterioration of physical structure in the soil is exceptionally rapid under East African conditions, and that it constitutes a factor of great importance which is closely connected with the vital matter of soil/water relations [19, 20]. As has already been observed, the effect of water shortage upon plant growth is much more marked under the prevailing climatic conditions than in the temperate zones, and it is very generally a critical factor in crop production. This recent work has also indicated that the use of a temporary pasture cover in the arable rotation provides a means of recovering and maintaining suitable soil structure, in addition to the more obvious fertility-building possibilities implied.

Although the effect of incorrect methods is less pronounced in areas of European farming, in part because the land is not densely occupied, it is essentially similar in trend so far as crop production is concerned, and there is urgent need to provide a means of restoring and safeguarding soil fertility, particularly in regard to structure. Temporary pasture should form the pivot of future crop rotations. It has to some extent been adopted, but under present conditions of sparse occupation, the conversion of extensive, inadequately fenced areas to the intensive methods implied in the proper use of such pasture is a costly process and one which cannot be effected without considerable delay.

The possibility of crop growing is confined almost entirely to the regions of the same two moister plant communities, Highland Grassland and Forest and Combretum—Hyparrhenia Scattered-Tree Grassland, together with parts of the narrow belt of coastal vegetation. In each of these regions, however, there are considerable areas in which the nature of the terrain, and often also scarcity of water supplies, limit the extension of cultivation. The management of natural grassland[1] will therefore remain of importance in these areas, even if correct intensive development is attained over the greater part of the regions occupied by the plant communities.

At the present stage of development of the European farming areas in these two communities, natural grassland under light utilization constitutes the main part of the vegetation. In the Highland-Grassland-and-Forest region the chief problem of management is the advance of

[1] Natural grassland implies open vegetation not established by artificial seeding. The ground vegetation consists of true grasses, other herbs, and shrubs. The drier the community the greater the proportion of shrubs, until in the Desert Scrub shrubs preponderate for most of the year.

the inferior coarse-grass phase dominated by *Pennisetum schimperi*, in both the more restricted area of the typical community and in the extensive transitional zone (see description of community). In the former portion of the region the maintenance of a productive Kikuyu grass (*Pennisetum clandestinum*)—clover sward demands carefully controlled intensive management, while in the transitional zone the dominance of desirable *Themeda triandra* and the suppression of the coarse-grass phase is dependent upon periodical burning of the herbage. This relatively moist region is capable of supporting a more intensive form of development than generally exists under the present utilization consisting of extensive holdings, and the coarse-grass problem should be approached through the adoption of ley farming, in which sown temporary pasture in rotation with other crops would exclude the coarse-grass phase of the succession.

The Combretum—Hyparrhenia Scattered-Tree Grassland, with higher temperatures than the foregoing community and with rainfall between 35 and 60 inches, also provides conditions well suited to the use of temporary grass in ley farming. This development must evidently largely replace the present practice of retarding the advance of thicket by the use of fire in the natural grasslands, and it is already an urgent necessity in the areas of dense native agricultural occupation. In addition, the high-grass elements of this vegetation can be suppressed in favour of more readily utilizable herbage species by the control of fire in conjunction with fencing and suitable intensive management of the natural grassland.

The extensive Acacia—Themeda Scattered-Tree grassland, situated between 4,000 and 6,500 feet in Kenya, and with erratic rainfall of from 20 to 30 inches per annum, is adapted to light pastoral utilization. Only at the fringe of the type, where transition towards the moister adjoining communities is taking place, is crop production feasible. The greater part of the community is occupied by native pastoralists, but it also includes areas of European ranch holdings important to the stock industry of the country. In general, water-supplies are deficient, and in the main part of the region the chief effect of utilization is seen in considerable areas of deteriorated vegetation in the vicinity of permanent water. This results from a continually increasing stock population induced by the protection afforded by disease control and the cessation of tribal warfare. The requirements of progress are increased and better distribution of water-supplies, control of stock numbers, and the gradual introduction of rotational utilization based upon seasonal migrations between different vegetational areas. In this vegetation grass fires have an important effect upon the chief constituents of the community, as already explained. The influence of this factor in relation to the advance of bush and tree growth and also to the maintenance of *Themeda triandra* as the chief herbage dominant must be appreciated in connexion with plans for improvement, and it should form the subject of further research. In addition to the deterioration caused by grazing animals, a more important effect of incorrect utilization is increasing in parts of this region, where agricultural tribes have been permitted to extend

their crop-growing activities into conditions which are incapable of supporting them without destruction of the vegetation and rapid soil deterioration. This urgent problem arises from the increasing pressure of population in the neighbouring moister plant communities.

The lower-lying plains which constitute the greatest area of the East African territories and at least two-thirds of Kenya, support semi-desert vegetation consisting mainly of Desert Grass—Bush-and-Desert Scrub. The conditions of deficient moisture resulting from low and erratic rainfall together with high evaporation in these communities, permit the occupation by pastoral tribes only on a nomadic basis. The effects of utilization are similar to those observable in the foregoing Acacia—Themeda grassland, except that the greater scarcity of water results in more marked effects from concentration of animals near permanent supplies. Furthermore, in the extremely dry conditions there is a greater degree of instability in the vegetation/soil relationship, resulting in a delicate balance which is easily tipped towards deterioration by the smallest undue concentration of grazing animals. It is evident, in fact, that the cover of vegetation in the Desert Scrub is often insufficient to prevent continual tendency to movement at the soil surface under the influence of wind. This has been observed at points far removed from water where little or no utilization is possible. The chief problem is that of an increased population of domestic animals. Any plan for improved utilization must presuppose reduction and control of the numbers together with improved distribution of permanent water. Given these provisions, management designed to maintain the vegetal cover can be based effectively upon seasonal migration between areas of the Desert-Grass—Bush and the Desert-Scrub communities. The former, which contains sparse perennial grass, being reserved mainly for dry-season utilization, and the Desert Scrub, with its ephemeral growth of annual herbs and browse available from the bush, providing the wet-season grazing ground. It is noteworthy that where sufficient supplies of water exist, the condition of animals in this vast semi-desert region is often surprisingly good. The probable explanation lies in the fact that rapid desiccation of the herbage precludes leaching of nutrients to a marked extent, coupled with the observable fact that the extremely dry conditions result in a relatively very light incidence of intestinal parasites in the animals. Both these sources of loss are important in the regions of plant communities subject to protracted rainfall. Apart from scarcity of water-supplies, utilization is also limited in parts of the semi-desert region by the presence of animal trypanosomiasis transmitted by the tsetse fly. This is the case in the southern part of the Desert Grass—Bush approaching the coastal vegetation, throughout which the fly is distributed, and also in riverine vegetation to the north in both the Desert Grass—Bush and the Desert Scrub.

The Classification of the Ecological Regions in Relation to Development

The essential hypothesis of the approach made to development in this paper is that the environmental complex represented by each of the well-defined plant communities is substantially the same throughout the

distribution of the community. Where it is virtually unaltered by human agency or altered only to a calculable degree, the community is in fact the record of its environment over a long period of time. Such major units of vegetation are easily recognizable in East Africa, and the clearly marked connexions with various forms of life support the evidence of the vegetation in defining the ecological regions.

The classification provides an essential basis upon which to appreciate and assail the problems of development in this part of Africa. Progress towards the management of the vegetation itself, which is urgently required to combat advancing soil erosion, demands the separate treatment of the major communities which react differently to the various forms of utilization. In this connexion, the natural grasslands of each region require individual investigation. Furthermore, experience has already shown that the important advance to the use of temporary pasture in the areas of arable agriculture must depend almost entirely upon indigenous species, and that these are best used within the environment of the community to which they naturally belong. A centre for the investigation of agricultural problems in each of the main ecological regions is, therefore, a necessity. In view of the fact that results so obtained can be expected to apply throughout the area of each vegetation type concerned, this plan is not over-ambitious, and it might well result in a reduction of the existing establishment which has grown with a view to political rather than ecological needs. Particularly is this the case if the territories of the whole East African region are considered together.

The implications of the approach outlined extend far beyond the requirements of agricultural research and soil conservation, although these are, of course, fundamental to progress in other directions. There is a readily discernible relation between the vegetation types and various forms of human culture, ranging from dense agricultural activity to nomadism. Similarly, the distribution of wild and domestic animal species is clearly related to the major plant communities. With this distribution of people and animals is linked the distribution of diseases which also limit development, and the insect vectors of disease are often closely associated with definite types of vegetation just as are some of the larger animals. A matter of considerable importance to the East African territories is the preservation of the fauna, which is threatened by advancing land use and which, apart from aesthetic considerations, is an important source of revenue through the tourist traffic, particularly that of Kenya. Because of the well-defined environmental requirements of many of the animals, this project can be successfully based only upon an ecological classification of the region. The linkage between certain animals and vegetation types is, in fact, so clearly marked that 'animal indicators' are often of value in determining the plant communities. In view of the connexion between forms of human culture and the ecological regions defined by the vegetation, it appears evident that if full weight could be given to the classification as a basis for future plans, administration might be assisted by the avoidance of unsatisfactory political boundaries.

Thus, a consideration of the various implications of this classification

to which brief reference has been made, suggests that it provides a common ground which might induce a greater degree of co-ordination than has hitherto existed between the work of investigators in several different, though allied, fields. This aspect is of great importance, and it provides exceptional opportunity in a region where development is as yet in the early stages. An exhaustive account of the ecological regions is not intended in this paper, but an important object is to present the classification as an essential foundation for developing and conserving the natural resources, and to suggest extension of this approach by collaboration with other territories and national administrations in Africa.

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FIG. 2. HIGHLAND GRASSLAND AND HIGHLAND FOREST
Timboroa, west of the Rift Valley. Showing patchy distribution of forest

FIG. 3. HIGHLAND GRASSLAND AND HIGHLAND FOREST
S.E. of Mount Kenya, under African agricultural occupation

FIG. 4. SCATTERED-TREE GRASSLAND: LOW TREE—HIGH GRASS
Cherangani, N.E. of Kitale. *Erythrina tomentosa* with fissured, corky bark in foreground

FIG. 5. GROUPED-TREE GRASSLAND
West of Mara River. Isolated tree groups on old termite mounds

FIG. 6. COASTAL HIGH GRASS—BUSH
20 miles north of Mombasa. Showing scattered Baobab trees (*Adansonia digitata*)

FIG. 7. COASTAL HIGH GRASS—BUSH
North of Mombasa. Seasonal swamp with branched *Hyphaene coriacea* and tall herbage dominated by *Hyparrhenia rufa*

FIG. 8. SCATTERED-TREE GRASSLAND: ACACIA—THEMEDA
Laikipia Plain N.E. of Rumuruti

FIG. 9. TARCHONANTHUS—CYNODON ASSOCIATION
On ancient lake bed in Nakuru region of the Rift Valley

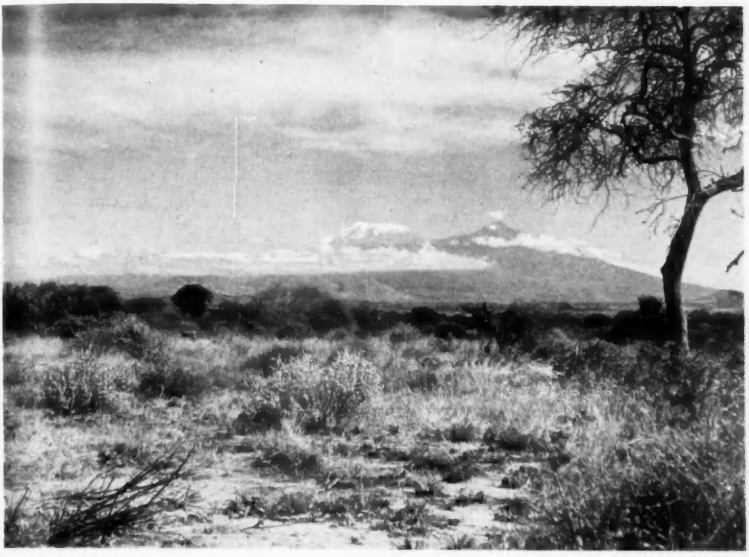

FIG. 10. DESERT GRASS—BUSH
Near Tanganyika border, Mt. Kilimanjaro in background

FIG. 11. DESERT GRASS—BUSH
North of Tana River. Showing *Delonix elata* of the scattered taller trees and Commiphora dominating the bush

FIG. 12. DESERT SCRUB

Muddo Gashi, north of Uaso Nyiro River. Showing Commiphora and Acacia. The grass herbage consisting of annual Aristida species is temporary and results from abnormally high rainfall in 1951

FIG. 13. DESERT GRASS AND DESERT SHRUB

N.E. of Isiolo. The most common, lava-strewn soil type of this community

STUDIES ON SUBSOIL PLACEMENT OF FERTILIZER AT URAMBO, TANGANYIKA TERRITORY

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Summary

Analyses of the depth-distribution of the most important plant-nutrient elements in the soil, in connexion with a study of root development of crops on the main soil types in the Urambo area, have led to conclusions which may necessitate a radical change in the method of application of phosphatic fertilizers in that region.

It was found that in all the soil types, phosphates and calcium, but not magnesium or potassium, were concentrated in the top soil, which varies in depth between 6 and 8 inches. The accumulation of phosphates in the top soil was greater in the grey sands than in the red sandy loams.

Root development differed greatly in these soil types. On the loams the roots of soya beans, for example, were equally distributed through the whole of the soil profile and might go down many feet, whilst on the sands, under equally dry conditions, and in the absence of any obstructions to deep rooting, the roots were confined to the top soil. It appeared likely that these differences in depth of rooting were due to the different distribution of phosphates between top soil and subsoil in the sands as compared with the loams. This suggested that a better response to phosphatic fertilizers may be expected through placing them in the subsoil. Field experiments on Urambo grey sands were carried out to test this hypothesis.

The yield of soya beans was increased above that of the controls receiving no phosphatic fertilizer by an average of 80 per cent. when concentrated superphosphate at the rate of 1·33 cwt. per acre was placed in the subsoil 12 inches below the surface. For maize, similarly treated, the average increase in grain yield was 45 per cent. No responses were recorded if the same dressing was either broadcast or drilled at planting time in two side-bands on either side of the seed-row.

THE application of fertilizers may be carried out in several ways. During recent years much attention has been given to fertilizer placement. In many instances better responses are obtained from this method than from ordinary broadcasting or other methods in which the fertilizer is incorporated with the surface layers of the soil.

Investigations on the root development of field crops, in connexion with soil-profile analyses, have led the author to study the method of deep placement, which may result in considerably better fertilizer responses. Similar results have been reported from the U.S.A., where the new technique has been described as 'double deck farming'.

Description of the Urambo Area

Urambo is situated on the East African plateau at an altitude of approximately 3,500 feet. Meteorological data are scanty. The average annual rainfall is believed to lie between 30 and 40 inches, falling from the end of October until the beginning of May. The dry season is quite rainless.

The area around Urambo is a well-marked peneplane. There are no

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incised water-courses and distinct hills are few and far between. Drainage lines widen out to huge flats that may be several miles across. These serve as temporary reservoirs for surface water run-off. The main rock is a coarse granite of the Basement Complex. Outcrops are scarce.

The uplands are covered with the deciduous Brachestegia-Isoberlinia open woodland, locally known as miombo. The woodland floor is covered with grasses. The vegetation of the drainage channels is determined by the frequency and the intensity of the seasonal flooding. As the flooding effects increase, trees become less frequent until eventually only grasses are found on the flats. In the dry season grass fires sweep through the woods and over the flats.

Soil-Profile and Root-Development Studies

The upland soils [1, 2, 3] are distinguished from the valley and drainage-channel soils in that they never suffer from the results of excessive run-off. There are two main groups:

1. Red Sandy Loams.
2. Grey Sands.

The Red Sandy Loams are situated at the upper part of the slope. Farther down the soils change into the Grey Sands, which are eventually succeeded lower down by the complex of valley and drainage-channel soils.

Red Sandy Loams.—These are equivalent to Milne's non-laterized red earths. They are many feet deep and well drained. The colour of the subsoil varies between pink and dark red. The top soil, between 6 and 8 inches deep, has a brownish tinge due to the presence of some organic matter. Top soil and subsoil gradually merge into one another. There are no impervious layers. The clay content of the subsoil is always a few per cent. higher than that of the corresponding top soil. The soils have a massive structure which can be turned into a simple grain structure by tillage. During the off season the soils dry out hard. Clearly they are well-matured eluvial soils, not necessarily derived from the rock which directly underlies them.

Grey Sands.—In Milne's classification these soils appear in the group of plateau soils. They are 20 feet deep or more and well drained. The change over from the 6 to 8 inches of dark-grey top soil to the pale yellow to almost colourless subsoil is sharply defined. The clay content increases gradually with depth but hardpans or impervious layers are absent. The soils have a simple grain structure and tillage operations can be done all the year round. These soils have been derived from locally transported material.

The mechanical and organic-carbon analyses of a characteristic profile of each of these soils are given in Table 1. The data for subsoil refer to samples taken between 34 and 38 inches below the surface.

Chemical analyses were carried out on twelve profiles of each soil. The Morgan soil-testing system [4] was used for the estimation of 'available' P, K, Ca, and Mg. The soil reaction was estimated electro-

metrically with the glass electrode in a 1 : 2·5 air-dry soil : water suspension. The average results are given in Table 2. The subsoil samples were taken from a 4-inch layer just below the transgression zone.

For both types of soil the distribution of cations through the profile is much alike. The distribution of potassium and magnesium is irregular; there are no distinct horizons of accumulation or impoverishment for

TABLE 1. *Profile Analyses of Red Sandy Loam (R.S.L.) and Grey Sand (G.S.) at Urambo*

Per cent. of oven-dry fine earth

	R.S.L.		G.S.	
	Top soil	*Subsoil*	*Top soil*	*Subsoil*
Clay, $< 2\,\mu$	23	25	5	11
Silt, 2–20 μ	2	2	2	2
Fine sand, 20–200 μ	37	39	32	40
Coarse sand, $> 200\,\mu$	38	33	60	46
Organic carbon	0·6	nil	0·5	nil

either element. Calcium and phosphorus have been accumulated in the top soil, but whereas the difference in calcium content between the top soil and the subsoil is of the same order for both types of soil, for phosphorus this difference is much greater in the sands than in the sandy

TABLE 2. *Chemical Analyses of Red Sandy Loam and Grey Sand at Urambo*

Depth in inches	*pH*	*Available nutrients (Morgan method) p.p.m./oven-dry fine earth*				*Remarks*
		P	K	Ca	Mg	
Red Sandy Loam						
0–6	6·2	0·25	11	77	9	top soil
10–14	5·3	0·10	12	12	8	subsoil
Grey Sands						
0–6	6·5	0·80	5	82	10	top soil
10–14	5·7	0·02	6	18	9	subsoil

loams. In both soils the pH falls with depth. The most marked differences between the top soils of the two types of soil are shown by their contents of phosphorus and potassium.

The fertility status of the upland soils.—The crops used in preliminary field trials were groundnuts, soya beans, sunflowers, maize, and sorghum. The potassium, calcium, and magnesium status of the arable soils seems to be high enough for the optimum growth of these crops. No positive responses have been found to potassic fertilizers, nor to liming with a dolomitic limestone or slaked lime. There also appears to be no shortage of trace elements; spraying trials with a range of minor elements did not

give any apparent differences in yield. Available nitrogen is extremely scanty. Non-leguminous crops yield well only if they receive a nitrogenous fertilizer. Leguminous crops nodulate freely.

Positive responses to superphosphates and various other phosphate fertilizers have been infrequent and usually small. Generally the sandy loams show smaller and less frequent responses to phosphate fertilizers than the sands. This is illustrated by the results of eleven trials on the former and eight on the latter, carried out in 1949–50 with groundnuts. The fertilizer was applied at planting time in two bands 1½ inches on either side of the seed-row and approximately at the same depth as the seed. On the sandy loams, application of superphosphate (18 per cent. P_2O_5) at 2·8 cwt. per acre was followed by yields averaging 35 lb. more than the average yield of 720 lb. of kernels per acre without fertilizer. For the sands, with the same treatment, the yield was 140 lb. more than the control yield of 930 lb.

The root-development of field crops in relation to soil-type.—During 1950–1 the rooting habits of the main field crops were studied on full-grown plants. Trenches were dug alongside a row of plants. The soil was carefully excavated with a spoon and where necessary it was washed out with a jet of water so as to expose the root system. Fig. 1 gives a schematic representation of the most important observations.

For *maize*, *sorghum*, *millet*, imported and native *grasses*, the root systems were alike, and similar on both types of soil, with no tap root. All the laterals and adventitious roots were equally well developed, with many second-order roots. Maize roots spread horizontally at least 3 to 4 feet, and downwards to at least 6 feet. Dwarf sorghums had a slightly smaller root system. The rooting habits of the tall varieties were rather similar to that of maize; the various grasses showed many variations. The most important feature of this group of crops is the absence of noticeable differences in the root systems as between the two soil types. The same was true of some other crops. The tap root of *sunnhemp* (*Crotalaria juncea*) reached a depth of 3 feet on both types of soil. Laterals were found along the whole of the tap root, spreading horizontally about 1 foot. For *velvet bean* (*Stizolobium* sp.) the tap roots were found as deep as 6 feet or more on both types of soil with laterals spreading to 3 feet.

With *cotton*, provided the soil was well aerated, the tap root penetrated the subsoil to a considerable depth. On a low-lying grey sand with a permanent water-table at a depth of 4 feet and which was completely saturated below 3 feet, the tap root grew to a depth of 2·5 feet. If the oxygen supply becomes limited at a shallow depth the tap root bends sharply and continues to grow horizontally. Very marked examples of this were found also on the red sandy loams in places where the micro-relief favoured temporary waterlogging. In such cases the whole of the root system was confined to the top 12 inches, whereas normally the roots grew down to at least 4 feet. Even under favourable conditions, on both types of soil, the numerous horizontal laterals did not spread more than 1 foot from the plant.

A second group of crops may be distinguished, in which marked

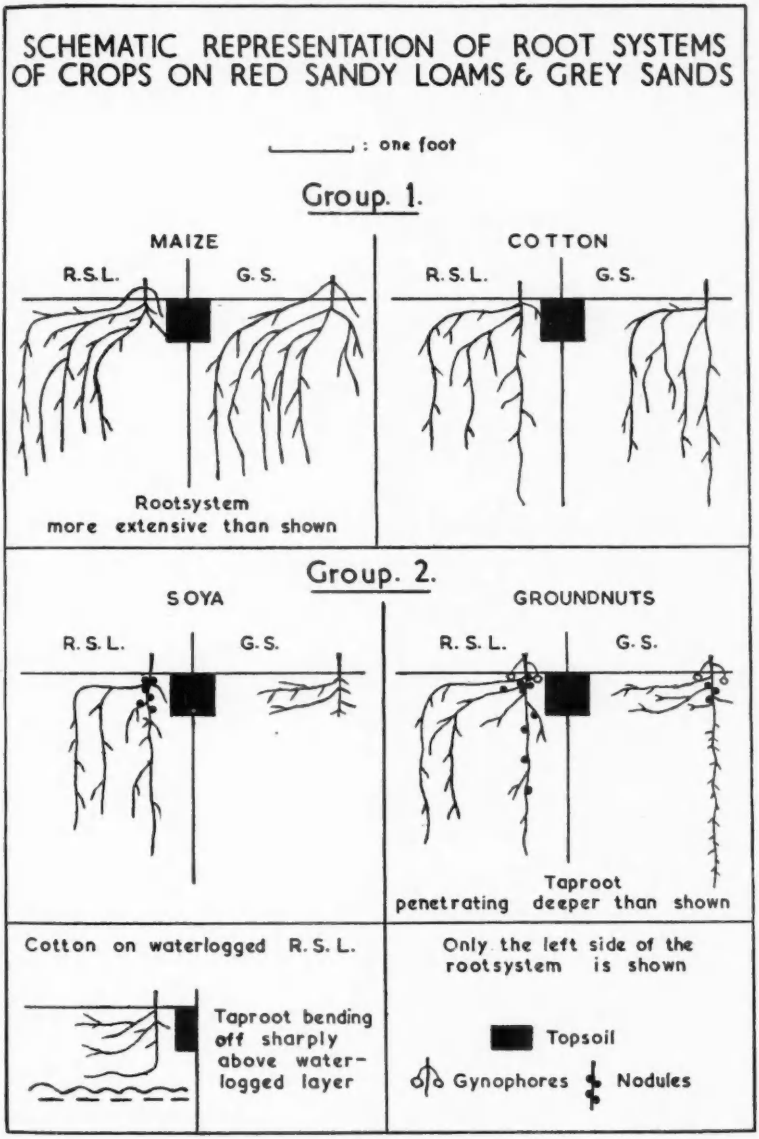

FIG. 1.

differences in rooting habit were related to soil types. With *soya beans* on the red sandy loams the well-developed tap root penetrated the subsoil to a depth of 2 feet. Directly beneath the soil surface the diameter

gradually tapered from 5 mm. at the crown to not more than 1 mm. at 1 foot depth; farther down the tap root was almost fibrous. Many laterals branched off over the whole length of the tap root; the longer ones at the higher levels, even the thickest ones, with an initial diameter of 2–3 mm., thinned out to a fibre at about 4 inches from the tap root. They did not penetrate deeply but grew more or less horizontally, with a maximum spread of 1 foot from the tap root. Most of the nodules were just above the point where the first laterals branched off, with an occasional one farther down the tap root or on the laterals. The nodules had a wart-like appearance, not exceeding about 1 centimetre in diameter. Tertiary roots were all very fibrous.

On the grey sands the root-system of soya beans had a totally different appearance. No roots were found in the subsoil; the whole root system was confined to the 'humic' top soil. The tap root showed only limited development with a constant diameter of 5 mm., abruptly thinning out to a fibre just touching the subsoil. Laterals branched off at the top of the tap root and grew only horizontally. As on the other type of soil, they were largely fibrous and spread at most 1 foot from the plant. No nodules were found, although all soya bean seed was treated with a commercial Rhizobium inoculant before planting, and contrary to the lush and well-developed growth on the red sandy loams, on the grey sands the soya beans showed severe symptoms of nitrogen deficiency.

Sunflowers behaved very similarly. On the red sandy loams tap roots went down at least 6 feet. Many long laterals branched off chiefly from the top 4 inches of the tap root; they spread horizontally and obliquely for a distance of 3 feet from the plant. On the grey sands the whole root system was confined to the 'humic' top soil. The tap root did not exceed 6 inches and all the laterals grew horizontally with a maximum spread of 2 feet from the plant.

Groundnuts showed a slightly different picture. In both types of soil the tap root penetrated to a depth of at least 6 feet. The maximum diameter was about 5 mm., tapering markedly with depth. In the red sandy loams the tap root had a woody appearance throughout and at the end, which was almost fibrous, it was strongly lignified. On the other hand, in the grey sands, only the upper part of the tap root, growing in the 'humic' top soil, was woody; lower down its appearance was fleshy with only slight lignification. Laterals longer than 1 inch originated mainly between 1 and 4 inches below where the lowest gynophores were implanted. In the red sandy loams these laterals penetrated the subsoil to the same depth as the tap root, whereas in the grey sands they grew in the top soil only. Their maximum spread was about 1·5 feet from the plant. Laterals shorter than 1 inch were found over the whole length of the tap root. On the red sandy loams they were woody and fibrous, but on the grey sands they remained fleshy, and were much shorter and thicker. All the laterals of groundnuts growing on the red sandy loams produced very fibrous tertiary roots; on the grey sands this occurred only with the long laterals growing in the top soil. Nodulation occurred mainly on the tap root, with only a few on the long laterals. In the red sandy loams nodules were found down to a depth of 2·5 feet, although

most were confined to the top soil, but in the grey sands scarcely any nodules occurred in the subsoil. On both types of soil the nodules did not exceed 3 mm. in diameter.

Summarizing the above, two groups of field crops have been recognized:

1. Crops with root systems which did not differ visibly whether they were grown on the red sandy loams or on the grey sands. This group includes maize, sorghum, and other grasses, cotton, sunnhemp, and velvet bean.
2. Crops with rooting habits which differed sharply according to the type of soil in which they were grown. In the red sandy loams root development took place throughout the whole of the soil profile, whilst in the grey sands either the whole of the root system (soya beans and sunflowers) or most of it (groundnuts) was confined to the 'humic' top soil.

Discussion.—No physical differences in the profiles of the two soil types that would account for the observed differences in rooting habits of sunflowers, soya beans, and groundnuts, as described above, could be detected, nor were there any grounds for ascribing these differences to waterlogging, which did not occur on the sites where the crops used in these studies were grown. Nevertheless, the rooting behaviour of the crops in group 2 was distinctly related to soil type, and the absence of roots in the subsoil was found only with the grey sands.

If the values for P, K, Ca, and Mg, as estimated with the Morgan soil-testing system, may be considered a measure of the amounts of these elements available for plant growth, the results of the profile analyses supply a possible explanation for these differences in rooting habits. It appeared that the lack of roots of the group 2 crops in the subsoil of the grey sands could be ascribed to the very low content of available phosphates in the subsoil as compared with the corresponding top soil. Although an accumulation of phosphates was found in the top soils of the red sandy loams, more phosphate was found in their subsoils than in those of the grey sands. The *relative* accumulation of phosphates in the top soils of the sands was much greater than in the loams.

If the above suggested explanation is correct, soya bean and sunflower roots may be expected to penetrate deeper in the sands if phosphates are placed in the subsoil, and this could be expected to lead to greater and more frequent responses to phosphatic fertilizers. Moreover, such possible benefits from the deep placement of phosphates would not necessarily be confined to the crops of group 2. Even maize, sorghum, and other crops of group 1 may benefit from this technique. It is also not unlikely that crops grown on the loams would respond better to deep-placed phosphatic fertilizers. Field experiments described below were carried out to investigate this question.

Field Experiments with Fertilizers

Preliminary trials.—In 1951–2 two observation strips were laid out on the grey sand, with dressings of concentrated superphosphate 45 per

cent. P_2O_5 at a rate of 2 cwt. per acre applied in different ways. For treatments D, S, and SS trenches 4 inches wide were dug by hand to the required depths. Soil layers taken from different depths were kept well separated and special care was taken to avoid mixing them. When the trenches were refilled each soil layer was replaced at the same depth as that from which it had been excavated. The treatments were:

T: Superphosphate placed in one band, 1½ inches from and parallel to the seed-row and at the same depth as the seed (i.e. 1–2 inches deep, without previous trenching).

D: Trenched to a depth of 20 inches (as for treatment SS) but then refilled, after which superphosphate was applied as in treatment T.

S: Trenched to a depth of 8 inches and superphosphate placed in one band 8 inches deep (just into the subsoil); trench then refilled and seed sown in a row vertically above the buried superphosphate.

SS: As for S, except that the soil was trenched to a depth of 20 inches and superphosphate buried at that depth.

The test crops used were sunflowers (var. Polestar) and soya beans (var. Benares). Each plot had four rows 10 feet long and 28 inches apart. Three weeks after germination the sunflower plots received a top-dressing of sulphate of ammonia at the rate of 4 cwt. per acre. The soya bean seed was treated with a Rhizobium inoculant. The treatments were not replicated.

The visible effects of the buried fertilizer were very striking on both strips. Both crops grew much more vigorously where the superphosphate had been placed in the subsoil. Trenching, with application of fertilizer at the surface (treatment D), had no visible effect. The plots on one strip were used for a study of the root development. Measurements were carried out on plants growing on the other strip. Data were collected from thirty plants for each treatment, chosen at random. Yield data were collected only for soya beans. The results are given in Table 3, which shows the mean differences between each of the other treatments and treatment T. The mean heights of sunflower and soya bean plants grown with treatment T were respectively 32 and 16 inches. The mean yield of soya beans grown with treatment T was 2·71 grammes per plant.

The data of Table 3 confirm the visual observations. Both sunflowers and soya beans grew more vigorously and a substantial increase in the yield of soya beans was associated with deep-placement of superphosphate.

Examination of the root systems of both crops showed root penetration approximately down to the depth at which the superphosphate had been placed (treatments S and SS). Plants for which fertilizer was placed in the top layers (treatments T and D) again showed a complete absence of roots in the subsoil. Further observations on the rooting habits of sunflowers and soya beans showed that in the early stages of growth these crops developed a thin and quickly growing tap root. A few days after

emergence this downward-growing 'feeler' had penetrated the subsoil. At this stage no lateral roots had been formed. Apparently, if an adequate supply of phosphates is available in the subsoil, the tap root thickens and continues to grow, and laterals that are developed later also penetrate the subsoil. On the grey sand this was the case only if phosphatic fertilizers had been placed into the subsoil. On the red sandy loam the subsoil supply of phosphates would appear to be enough for the root systems to follow this pattern of development even if no fertilizers are applied. In the absence of sufficient available phosphates the part of the 'feeler' that penetrated into the subsoil of the grey sand must have died off; laterals did not enter the subsoil and after a few weeks the root system was confined solely to the top soil in which most, if not all, of the available soil phosphates were concentrated.

TABLE 3. *Differences between Plants Grown with Treatments D, S, and SS and those grown with Treatment T*

Treatment	Extra length of stem, in inches		Extra yield of soya beans per plant, in gm.
	Sunflowers	Soya bean	
D	1	1	0·5
S	3	3	2·9
SS	17	9	3·8

Where a trench was dug but the fertilizer was then applied to the top soil (treatment D), only a few plants showed roots that had entered the deeper layers; most of the plants only had roots growing in the top soil, as if no trench had been dug. In each exceptional case where roots were observed to have grown into the deeper layers some 'humic' top soil was found there as well, which must have been dug in accidentally when refilling the trench. The few plants on treatment D with roots growing in the subsoil probably account for the slightly higher figures found as compared with treatment T.

There is little doubt that the deep placement of superphosphate had resulted in a better performance of the two crops. Apparently the results obtained with the Morgan soil-testing system were indicative of the availability of the main nutrients tested. The better performance with deep placement of superphosphate was not necessarily due only to an increased supply of phosphates. The more extensive root system obtained with subsoil fertilizer placement, penetrating deeper into the soil, probably enabled the plants to take up more nutrients in general. Also, especially during periods of drought, the water-supply is better secured. With legumes the greater availability of phosphates would lead to better nodulation and an increased supply of nitrogen. The soya-bean plants that had been grown with superphosphate applied to the surface soil (treatments T and D) looked yellow and very nitrogen deficient, whereas those grown with deep-placed fertilizer were a fresh green without any sign of nitrogen deficiency.

Counts showed that such increased nodulation had occurred on the

plants grown with deep-placed phosphate. Table 4 shows the number of nodules per twenty-five soya-bean plants. The nodules of soya bean break off very easily, and in lifting the plants a fair number of nodules must have been lost. Consequently the numbers counted should be regarded as less than the actual numbers on the plants.

TABLE 4. *Counts of Root Nodules on Soya-bean Plants Grown with Different Treatments*

Treatment	*Number of nodules per 25 plants*
T	4
D	6
S	18
SS	30

Replicated Experiments.—In 1952–3 two replicated field experiments were conducted on the grey sandy soil with soya beans and maize, of similar design and treatments. They were situated close together on land which had been cropped in the previous season with groundnuts and which had then received concentrated superphosphate at a rate of 1 cwt. per acre.

The soya beans (variety Benares), which had been treated with a Rhizobium inoculant, were grown in rows 28 inches apart and 7 inches apart in the rows. The maize (variety Katumbili) was grown in rows 36 inches apart and 14 inches apart in the rows. The plot-size was 0·0105 acres for soya beans and 0·0135 acres for maize.

Treatments:

The layout was a 6×6 latin square. Besides the 'No phosphate' (Control) treatment, there were five phosphate treatments: concentrated superphosphate (45 per cent. P_2O_5) at a rate of 1·33 cwt. per acre (0·6 cwt. P_2O_5 per acre) was applied in the following five different ways:

Broadcast and disk-harrowed shortly before planting.

Placed (*surface*) in two bands, 1½ inches on either side of the seed-row and at the same depth as the seed (approximately 2 inches below the surface).

Deep-placed, 6 inches below the surface in one band underneath the seed-row (at the bottom of the 'humic' top soil).

Deep-placed, 9 inches below the surface in one band underneath the seed-row (in the upper layers of the subsoil).

Deep-placed, 12 inches below the surface in one band underneath the seed-row (deep in the subsoil).

The deep-placement was carried out in the same way as described above for the preliminary trials. The maize experiment received three top-dressings of sulphate of ammonia, each at a rate of 1 cwt. per acre.

In the soya-bean experiment the effects of the deep-placement treatments were clearly visible; the plants grew more vigorously and the leaves were darker green; defoliation was distinctly slower. In the maize experiment no treatment effects were visible.

Of the six rows of plants on each plot of the soya-bean experiment, the

two outer rows were discarded and the yields of the remaining four rows were recorded (effective plot size 0·007 acres). The maize yields recorded were those of the whole plots as planted. The mean plant populations for soya beans and maize in thousands per acre were respectively 31·4 and 12·2.

The yield results of both experiments are given in Table 5.

Except for the 'deep-placement, 12 inches' treatment, the yields from the treated plots do not differ significantly from those of the control (no phosphate) plots. However, the 'deep-placement, 12 inches' plots gave highly significant increases in yield at the rates of 410 lb. per acre (82 per cent.) for soya beans and 985 lb. per acre (43 per cent.) for maize.

TABLE 5. *Yields of Soya Beans and Maize with Different Methods of Placement of Superphosphate*

Treatments	*Soya beans*	*Maize*
	Wt. of beans lb./acre	*Wt. of grain lb./acre*
Control (no phosphate)	500	2,316
Phosphate, broadcast	505	2,311
Phosphate, placed (surface)	581	2,053
Phosphate, deep-placed, 6 inches	566	2,091
Phosphate, deep-placed, 9 inches	655	2,648
Phosphate, deep-placed, 12 inches	910	3,301
Minimum significant difference ($P = 0{\cdot}05$)	172	361

Discussion.—The possibility that the mere effect of trenching has contributed to the increases in yield in the replicated experiments cannot be ruled out, since these 'trenching alone' treatments were not included in experiments, and since trenched land adjoining the experimental area (believed to be more fertile) gave yields of soya beans similar to those obtained from the high-yielding plots of the experiments. However, the results of the preliminary trials tend to discount this possibility, and it may be concluded that deep-placement of superphosphate in the subsoil resulted in a better performance per plant. The effects were more noticeable on soya beans than on maize. This is in accordance with the difference in rooting habits between the two crops, which suggests that soya beans should respond to this technique better than maize. There is probably an optimum depth for subsoil fertilizer placement, which may exceed that at which the operation can be carried out satisfactorily by machine.

Similar results to those described above have been obtained in the U.S.A. [5, 6]. Dr. H. Kohnke reported to the author in a private communication that a variety of soil types, in particular a 'medium heavy silt loam' responded very well to subsoil fertilizer placement. It would appear that the usefulness of this new technique is not limited to the conditions which prevailed in the author's experiments. However, the investigations reported in this paper must be regarded as preliminary, and the conclusions tentative, until further experiments have been carried out.

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THE EFFECT OF AN ANTIBIOTIC SUPPLEMENT ON THE PROTEIN REQUIREMENTS OF FATTENING PIGS

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Summary

Treatments including high and low protein with and without a supplement of aureomycin, were given to different groups of Large White pigs.

Greater uniformity of growth was evident in the supplemented groups. A measure of protection against the visible effects of the condition associated with virus pneumonia was apparent in these groups.

Over the trial period as a whole both supplemented groups grew significantly faster than the low-protein control group. The performance of the unsupplemented group on high protein was only slightly and non-significantly less than that of the high-protein group receiving aureomycin. No significant differences were obtained for the efficiency of utilization of food, although the lowest figure was recorded for the low-protein control group.

Treatment effects on carcass quality were not marked, but slightly longer and leaner sides were recorded for high-protein groups.

Supplementation of a subnormal protein ration with aureomycin significantly increased growth rate by 13 per cent. This supplemented subnormal protein mixture gave performance figures higher than those obtained with the widely accepted, standard protein ration, but not significantly so.

Within the limits set by the conditions of the trial, evidence of the protein-sparing action of aureomycin as a supplement to feeding mixtures has been obtained.

EXTENSIVE research in the United States and other countries, including a number of large-scale trials in the United Kingdom under the aegis of the Agricultural Research Council [1], has established that the feeding of antibiotics has a beneficial effect on the growth and food economy of fattening pigs. The response to the feeding of an antibiotic is influenced by the disease level of the environment and by the diet [2]. It is with the diet, and in particular the protein requirements of fattening pigs, that the present investigation is concerned.

Woodman and Evans [3] have reported that, over the whole fattening period, a mixture containing as little as 5 per cent. fishmeal initially, and none after reaching 150 lb. liveweight, has given nearly as good results in terms of growth rate and food economy as a control mixture containing 10 per cent. fishmeal, although at the lower protein level the pigs had a temporary setback in the early stages. They suggest that a mixture containing 7 per cent. fishmeal up to 120 lb. liveweight and none thereafter, should provide adequate protein for maximum performance.

Hoefer, Luecke, Thorp, and Johnston [4] have indicated that our present standards of protein requirements for pigs may be too high when a terramycin supplement is included. Burnside, Grummer, Phillips, and Bohstedt [5] report that aureomycin increased performance when pigs were fed mixtures containing initially 16 per cent. crude protein or less, while Catron, Jensen, Homeyer, Maddock, and Ashton [6] state that they

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found no difference in daily gains for aureomycin-fed pigs on mixtures ranging in initial crude-protein content from 14 to 20 per cent.

Jensen, Ashton, Maddock, Homeyer, and Catron [7] report that in the early stages (36–75 lb. liveweight) pigs on a terramycin supplement gained significantly faster than non-supplemented pigs at all protein levels. When the whole fattening period was considered, however, neither terramycin nor aureomycin improved growth rate compared with the controls, but daily gains increased with increasing protein content of the ration up to 14 per cent. crude protein, irrespective of an antibiotic supplement.

In these trials the basic diets contained vegetable proteins, although in some cases vitamin-B12 supplements or fish solubles were included. Moreover, self-feeding (i.e. unrestricted feeding) was used.

From the foregoing evidence it appears that a saving in protein may be effected by incorporating an antibiotic supplement with the food mixtures, quite apart from a general reduction in a standard unnecessarily high. The experiment carried out at Wye College in the summer of 1952 was a preliminary approach to the problem of determining optimum protein levels under British conditions.

Experimental

The effects of feeding mixtures containing two levels of protein with and without an aureomycin supplement were compared. The food mixtures, and the scale of rationing according to liveweight were similar to those used by Woodman and Evans [3].

The four experimental treatments were:

I. Low protein.
II. High protein.
III. Low Protein+Aureomycin.
IV. High protein+Aureomycin.

Details of the mixtures used are given in Tables 1 and 2 and the scale of feeding in Table 3. The high-protein treatments are widely used in this country and, on the scale of feeding used, provide a generous margin of protein in excess of the minimum requirements suggested by Woodman [8], but the low-protein treatments were adopted to provide less than the generally recommended levels. Whereas the high-protein mixture contained 10 per cent. fishmeal initially, gradually diminishing to 5 per cent. at 150 lb. liveweight, the low-protein mixtures contained only 5 per cent. fishmeal at the outset and none by the time the pigs were 150 lb. in weight. The aureomycin supplement consisted of Aurofac 2A, containing 3·6 gm. of aureomycin per pound. With one exception, all the mixtures contained a variable amount of vitamin B12 from the Aurofac or fishmeal, so for the sake of uniformity a standard vitamin B12 supplement sufficient to cover requirements, was included in all rations, and 1 oz. of cod-liver oil per pig was added direct to the troughs once weekly. Details of the chemical composition of the feeding stuffs are presented in Table 2 as the mean values for the whole trial.

Five Large White litters were available for the trial, which was of

randomized-block design with five replications. Block selection on the basis of similar sex and weight within a single litter was found to be impossible. Pigs by the same boar but not necessarily out of the same sow

TABLE 1. *Feed Mixtures**

Weight range	*50–90 lb.*		*150–210 lb.*	
Treatment†	*I, III*	*II, IV*	*I, III*	*II, IV*
	%	%	%	%
Barley meal	64	60	69	64
Wheat offals	27	27	27	27
Dried lucerne meal	3	3	3	3
White fishmeal‡	5	10	0	5
Minerals§	1	0	1	1
Crude protein	13·8	16·7	11·1	13·8

* *Vitamin B12* added to all mixtures at the rate of 15 mg. per ton.

† *Treatments III and IV*. Aurofac 2A added at the rate of 4 lb. per ton (14·4 gm. aureomycin per ton).

‡ *Fishmeal* reduced at each 20 lb. liveweight increment from 90 to 150 lb. Barley correspondingly increased.

§ *Mineral mixture*: ground limestone 3 parts, common salt 1 part.

TABLE 2. *Average Chemical Composition of Feeding Stuffs*

	Barley meal	*Wheat offals*	*Dried lucerne*	*White fishmeal*
	%	%	%	%
Moisture	14·55	11·61	11·39	10·47
Crude protein	9·51	14·79	17·86	64·18
Ether extract	1·69	4·92	2·49	3·21
N-free extract	68·47	53·54	35·97	..
Crude fibre	3·30	10·33	22·41	..
Ash	2·48	4·81	9·88	22·14

TABLE 3. *Feeding Scale*

Liveweight lb.	*Meal lb./day*	*Liveweight lb.*	*Meal lb./day*
40	2·1	120	5·3
50	2·5	130	5·6
60	3·0	140	5·9
70	3·5	150	6·2
80	4·0	160	6·4
90	4·3	170	6·6
100	4·6	180	6·7
110	5·0	190	6·9
		200 and over	7·0

were therefore chosen. Within the five blocks, the pigs were allocated at random to the experimental treatments. Average initial liveweights for the four experimental groups varied from 48·8 lb. for the high-protein antibiotic group to 52·0 lb. for the low-protein antibiotic group. Average age at the start of the trial was 12 weeks.

The pigs were housed in an open yard. A large wooden shed provided sleeping quarters and covered individual feeding accommodation was available. The two antibiotic groups were segregated from the two non-supplemented groups by central partitions in the hut and yard.

The trial started on 13 May 1952 after a preliminary period of 13 days to accustom the pigs to individual feeding. The appropriate experimental mixtures were introduced on this date and feeding was strictly rationed according to the scale given in Table 3. The meal was fed twice daily in the form of a thick slop, water and meal being mixed up in the proportion of $2\frac{1}{4}$: 1 by weight. Additional drinking water was available. The pigs were weighed on three consecutive days at the beginning and at the end of the trial, and twice weekly throughout. Changes in food mixtures were made for individual pigs as they reached the appropriate weight. The trial finished when the thirteen heaviest pigs were sent to the factory. Full records and experimental treatments were maintained for the remaining pigs until they reached bacon weight. Following slaughter the cold carcasses were evaluated on the system used in the B.D.F.A. Dairy Show Bacon Carcass Competition.

Results

The results in terms of average gains and food economy for the entire experimental period, are presented in Table 4.

TABLE 4. *Average Gains and Food Economy (19 weeks)*

	Non-antibiotic	*Antibiotic*	*Mean*	*Sig. diff. (P = 0·05) between means*
Total gains (lb.)				
Low protein	145·1	163·4	154·3	5 pigs: 12·3
High protein	155·8	160·8	158·3	10 pigs: 8·6
Mean	150·5	162·1	..	
Lb. meal/lb. gain				
Low protein	4·00	3·75	3·88	N.S.
High protein	3·84	3·79	3·82	
Mean	3·92	3·77	..	

It was soon apparent that in one block the four pigs were unthrifty the pig on treatment I in particular consistently leaving food. Individual total gains for this block were only 118, 125, 144, and 144 lb. for treatments I to IV respectively. These poor performances have naturally influenced the general level of results. Withdrawal of this block was considered but it was thought that the antibiotic treatments might produce a noteworthy result and certainly the two pigs on antibiotics grew much better than the other two.

A fortnight after the trial started, a dry cough characteristic of chronic virus pneumonia infection was noticed among pigs of the unsupplemented groups. This continued throughout the trial to a varying degree, but only one antibiotic pig was ever observed coughing and this occurred the day after the trial finished. Two pigs on each of the non-supple-

mented treatments had periods of illness, typified by loss of appetite and some rise in temperature. In two cases the pigs recovered in 2 days, but the others took nearly 2 weeks. Apart from the two latter cases, which included the pig already mentioned which frequently refused food, refusals were few. It was noticed, however, that the antibiotic-fed pigs ate their rations more readily than the controls.

Individual food consumption varied considerably within treatments, partly due to the wide liveweight range; but treatment averages were not appreciably different, varying from 580 lb. meal for the low-protein non-

TABLE 5. *Average Daily Gains and Food Economy, 50–90 lb.*

	Non-antibiotic	*Antibiotic*	*Mean*	*Sig. diff. ($P = 0.05$) between means*
Daily gain (lb.)				
Low protein	0·83	0·92	0·88	N.S.
High protein	0·95	1·01	0·98	
Mean	0·89	0·97	..	
Lb. meal/lb. gain				
Low protein	3·42	3·16	3·29	5 pigs: 0·36
High protein	2·90	2·81	2·86	10 pigs: 0·26
Mean	3·16	2·99	..	

supplemented group to 613 lb. for the low-protein antibiotic group. At the end of the 19-week trial period mean liveweights ranged from 196·4 lb. for the low-protein control group to 215·4 lb. for the low-protein antibiotic group. Variation in total gains was appreciable, amounting to 43 and 44 lb. within the low- and high-protein control groups respectively. Within antibiotic groups there was better uniformity, the maximum difference being only 28 lb. and 33 lb. respectively for low- and high-protein pigs. It will be noted from Table 4 that both antibiotic groups grew significantly faster than the low-protein unsupplemented group, while both were slightly better than the high-protein control, though the differences were not significant. Efficiency of food utilization followed a similar pattern to total gains although no significant differences were obtained. Variation within antibiotic treatments was again less than in the unsupplemented groups.

In order to examine these factors in greater detail, the results have been analysed for two phases of growth as shown in Tables 5 and 6. It was not possible to consider the period after 150 lb., since one pig attained only 160 lb. liveweight when the trial ended.

Although intra-treatment variation was too great to reveal significant differences for growth rate, a comparison of the high-protein treatments for the two periods suggests that most of the antibiotic effect occurred in the earlier phase. In the case of food economy, for the earlier period from 50–90 lb., the influence of protein level was highly significant ($P = 0.01$) though there was more marked effect on the unsupplemented than on the antibiotic treatments. It is interesting to note that the antibiotic low-protein group, although having the best performance taking

the trial as a whole, was slightly inferior to the control high-protein group in this early stage. In the intermediate phase, from 90 to 150 lb., however, this group came to the fore, though there were no statistically significant differences.

The small number of pigs on each treatment and the wide variation in carcass weight made a detailed study of carcass quality impracticable and the results have not been analysed statistically. Generally speaking, the antibiotic treatment appeared to have little effect at either protein level, though the non-antibiotic group pigs had slightly longer sides and a tendency to thicker bellies. Rather more marked trends were noticeable between protein groups. High-protein groups, irrespective of an antibiotic supplement, had appreciably thinner backfat, slightly greater length, and better balance of side than low-protein groups. The latter appeared to have a slightly firmer fat as judged by touch, but this could be due to the presence of fishmeal in the high-protein mixtures throughout the fattening period.

TABLE 6. *Average Daily Gains and Food Economy, 90–150 lb.*

	Non-antibiotic	*Antibiotic*	*Mean*	*Sig. diff. ($P = 0.05$) between means*
Daily gain (lb.)				
Low protein	1·16	1·30	1·23	N.S.
High protein	1·26	1·28	1·27	
Mean	1·21	1·29	..	
Lb. meal/lb. gain				
Low protein	4·02	3·46	3·74	N.S.
High protein	3·67	3·69	3·68	
Mean	3·85	3·58	..	

Discussion

The inclusion of an unthrifty block of pigs and the presence of a condition which is presumed to be the virus pneumonia described by Betts [9] limit the value of the trial. Nevertheless, since the incidence of virus pneumonia would appear to be so widespread in commercial herds it is considered that the results obtained are of interest provided these points are borne in mind.

In the first place, the characteristic dry cough was not apparent in pigs receiving aureomycin even though they were separated from the non-supplemented groups by a wire fence only. It is unfortunate that a post-mortem examination of the lungs could not be made since the virus may have been present in the lungs of antibiotic-fed pigs although no clinical symptoms occurred. In contrast to the control groups, no illness occurred in the antibiotic groups, suggesting that the aureomycin at least gave protection against secondary infections normally associated with this condition. Although the unsupplemented low-protein group was not significantly slower-growing or less efficient than the corresponding high-protein treatment, for the trial period as a whole, this was probably due to the considerable variation between treatments. It is suggested

that certainly in the early phase, and probably for the whole period, under the specific conditions of the trial, a 5 per cent. fishmeal level was inadequate for maximum growth and thriftiness. In the 50–90 lb. phase, the unsupplemented low-protein group appeared to suffer from a lack of protein, though recovering rapidly from this initial handicap.

The aureomycin supplement appeared to be of significant value in improving the growth rate of pigs on a subnormal protein intake when the whole trial period is considered, performance being increased by 13 per cent. On a generous protein régime, the difference between the supplemented and non-supplemented groups was not significant and amounted to only 3·4 per cent. as compared with the general average of 10½ per cent. obtained in the Agricultural Research Council trials [1]. As for efficiency of food conversion, the advantage of aureomycin was less definite, although the low-protein antibiotic group had a 6·2 per cent. advantage over the non-supplemented low-protein group.

The results suggest that with the addition of an aureomycin supplement, mixtures including only half of the quantity of fishmeal normally fed, and containing approximately 80 per cent. of the normal crude-protein content, can give as good results as the more liberal protein level. In addition, it appears to have influenced uniformity of performance favourably, as indicated by appearance, growth rate, and food economy.

With regard to carcass quality no specific effects from aureomycin feeding have been reported in the literature. The evidence concerning the effect of protein level is conflicting, however. Woodman and Evans [10] report no adverse effects when low-protein diets were fed; Catron *et al.* [6] claim similar results, although admitting that all their pigs were very fat. A report from the U.S.D.A. [11] on the other hand states that an 18 per cent. protein level gave a higher proportion of lean to fat in carcasses than a 13 per cent. level, while a similar trend is mentioned by Jensen *et al.* [7] and by Wilson, Burnside, Grummer, and Bray [12]. The results of the present trial tend to support the latter view, though there is insufficient evidence to be conclusive.

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THE EFFECT OF INFREQUENT WATER INTAKE ON THE CONSUMPTION AND DIGESTIBILITY OF HAY BY ZEBU CATTLE

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Summary

Zebu oxen were fed an *ad lib.* ration of chaffed hay during a series of studies to test the effects of restricted water intake on digestive efficiency. The watering régimes were (*a*) *ad lib.* consumption whenever the animals wished; (*b*) water available for 1 hour every 48 hours; and (*c*) water available for 1 hour every 72 hours. These intervals were chosen to simulate conditions in the arid and semi-arid regions of East Africa.

With watering once every 48 or 72 hours respectively, the oxen drank 12·0 or 30·7 per cent. less water than, and the daily dry-matter consumption fell to 93·8 or 92·2 per cent. of the quantity eaten, when water was always available. These differences were all highly significant.

The only significant difference in the digestibility coefficients of the constituents of the hay rations fed on the different watering régimes was associated with the crude-fibre fraction. The average crude-fibre digestibility coefficients were 49·5, 53·0, and 53·5 per cent. for the periods in which watering was *ad lib.*, every 48 hours, or every 72 hours, and these differences were significant at the $P = 0{\cdot}001$ level.

In consequence of this higher digestibility of the crude fibre fraction, and in spite of the highly significant differences in food intake, the calculated starch-equivalent consumption was not significantly lower when watering only every 48 hours than when water was always available, but when watering was restricted to once in 72 hours a significant lowering ($P = 0{\cdot}05$) occurred.

A highly significant reduction ($P = 0{\cdot}001$) occurred in the amount of digestible crude protein available to the animals as the frequency of watering was reduced. The increased rate of crude-protein excretion in the faeces may have been associated with a need to lubricate the much drier excreta with mucus.

WHILE the presence or absence of tsetse-flies is undoubtedly the most important single factor controlling the distribution of livestock in East Africa, enzootic and epizootic diseases still further restrict the use of available grazings in the fly-free areas. Consequently, the more primitive native husbandman is capable of maintaining large flocks and herds only in the arid and semi-arid areas because, without veterinary aid, he is relatively helpless against the ticks, worms, biting-flies, and the many other parasites which ravage his animals in the wetter and better grazing areas. This concentration of animals into the drier regions, where conditions are less favourable to these parasites, is the logical reaction of primitive peoples who do not possess the knowledge necessary for combating the diseased conditions caused by these parasites. Inevitably this concentration into the drier areas exposes the animals to the annually recurring consequences of overstocking—undernutrition and deaths from starvation—but these are factors which are comprehensible and

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are the premiums such African husbandmen are prepared to pay for the survival of the greater proportion of their stock.

The availability of permanent water, within reach of primitive tools and skill, determines the distribution pattern of man and his animals in these more arid regions, where the erratic and sparse distribution of permanent water leads to unbalanced and heavy concentrations of animals. As the natural grazings in the vicinities of such permanent waters become progressively overstocked and bare, the animals have to spend longer and longer searching for food and their owners are forced to strike a balance between the time wasted from a grazing point of view and the need to allow their stock the necessary minimum quantity of water.

Typical of these conditions are the management practices in Masailand where the grazings around permanent waters are eaten-out relatively early in the dry season. The owners establish their dry-season homesteads around and approximately ten miles distant from the permanent waters and, as the season advances, graze their stock away from the water on one day and return to their homes the same night. On the second day the animals are herded over the eaten-out pastures to the water-holes and then return home in the evening. After a period, these peripheral grazing areas become denuded and inadequate so that the stock have then to be grazed out from the homestead to more distant temporary kraals, where they spend the night. The animals are brought back to the homesteads on the second night and are walked in to water on the third day. This is a very rigorous existence but, in spite of it, the Zebu cattle look better than would their European counterparts. The young and the aged are the first to lose condition and become thin and miserable but, as the season advances and grazings become more denuded, all types of animals lose weight and condition. Taking into consideration the long distances covered in the hot environment and the poor quality of the sparse grazings, it is at once apparent that the Zebu has an undoubted ability for surviving on a less frequent watering régime than European breeds.

Previous work in East Africa [1] has shown that, with constant access to water, the local short-horned Zebu cattle do not possess any significant digestive superiority over $\frac{3}{4}$-Ayrshire$\times\frac{1}{4}$-Zebu grades and it is regretted that an opportunity for a similar comparison with pure-bred European animals has not yet occurred. The present series of experiments was therefore conducted on the indigenous Zebu and sought to determine whether water shortage, or infrequent access to water, influences the capacity for or the digestibility of food. Such a severe system of restricted watering, as described above, applies only to local Zebu cattle living on dried-up herbage and 'standing' hays and this series of experiments was consequently conducted on an unsupplemented local-hay ration fed according to appetite. The experiments did not fully simulate the rigorous conditions of normal dry-season life in the more arid areas because the animals were confined to indoor digestibility crates and therefore did not suffer the hardship of long walks in the sun in search of food or water nor the disadvantages of being unable to secure their dry-matter requirements daily.

Description of Experiments

The trials were conducted at Mpwapwa in Central Tanganyika in 1941. The moist faecal samples were analysed immediately, but dry-matter analyses had to await suitable later opportunities. Six full-mouthed Zebu oxen were used, all of which had been previously used in digestibility work and were considered a comparable group of docile animals. They had all been stall-fed for 2 months before the trials started but had been allowed uncontrolled free exercise for some 5 hours daily in a concrete-floored yard, part of which was roofed over so that they could shelter from the sun. The animals were brought on to their respective watering régimes during this period and had been on the experimental procedures for 1 month before being put into the digestibility crates. Between successive trials the animals also had a month for

TABLE 1. *Watering Régimes in the Experimental Periods*

	Oxen A and B	*Oxen C and D*	*Oxen E and F*
16–27 Sept. 1941	*Ad lib.*	Every second day	Every third day
12–23 Nov. 1941	Every second day	Every third day	*Ad lib.*
8–19 Jan. 1942	Every third day	*Ad lib.*	Every second day

adjustment before being placed in the crates for the next series. The digestion studies were conducted on previously chaffed hay which had been thoroughly mixed before bagging for storage but, during the preliminary and intervening training periods, the animals were fed on unchaffed hay from the same stack. The objective was to avoid serious changes in the nature and composition of the hays fed in the respective trials. Twelve-day collection periods followed a 9-day preliminary feeding in the digestion crates, and water consumptions were recorded in 6-day units. The dates and watering procedures for the respective trials are given in Table 1.

This 3×3 layout for the experiment was chosen because a previous attempt [1] to investigate the reactions of three pairs of oxen adapted to differing watering régimes had given, in single digestibility trials for each pair, inconclusive evidence of any significant differences in digestive ability as a result of restrictions in water intake. Differences in food intake and digestibility between the individual animals might have affected these earlier results, and as the matter was of considerable practical significance in East Africa, a more thorough investigation was planned. This repetition was also desirable because Larsen, Hungerford, and Bailey [2] had previously found that, with a less severe but lengthening interval between waterings or when water consumption was restricted to half the volume which would normally be drunk, the digestibility of crude fibre was increased but that increases in the digestibility of crude protein and of nitrogen-free-extract components were less marked, and irregular. These earlier workers had fed a mixed ration of hay, silage, and concentrates to milking cows and it was important to learn whether the increased digestibility of fibre recorded by

them was due to the better ration, to the experimental procedure, or to the different type of animals employed.

In the present series, the chaffed hays were weighed out before each trial and composite samples taken for analysis. Nitrogen determinations were made daily on the moist faeces, and aliquot samples of the daily faecal excretions were dried and stored for subsequent analysis. The hays used in the three digestibility phases had the compositions shown in Table 2. The uniformity in composition shown by these analyses reflects the care taken to avoid unnecessary discrepancies between the chaffed hays used in the different digestibility trials.

TABLE 2. *Dry-matter Compositions of Hay per cent.*

	September trials	*November trials*	*January trials*
Crude protein . .	8·76	8·80	8·71
Ether extract . .	1·46	1·43	1·40
Crude fibre . . .	36·88	36·71	36·95
Nitrogen-free extract .	43·43	43·54	43·53
Total ash . . .	9·47	9·52	9·41

Results

As will be observed from the figures in Table 3, the appetites of the animals on the restricted watering were somewhat depressed and, in order to avoid large residues, the daily procedure was to add only

TABLE 3. *Dry Matter and Water Intakes during Digestibility Trials*

Ox	*Watering régime*	*12-day dry matter consumptions*			*Water consumption (per 6 days) litres*
		Fed kg.	*Residues kg.*	*Intake kg.*	
A	*Ad lib.*	54·0	1·7	52·3	74·7
	Every second day	50·0	1·4	48·6	64·4
	Every third day	48·2	0·4	47·8	49·6
B	*Ad lib.*	54·0	0·9	53·1	74·1
	Every second day	49·8	0·8	49·0	65·6
	Every third day	49·2	1·2	48·0	52·9
C	*Ad lib.*	54·0	0·6	53·4	75·1
	Every second day	50·8	1·0	49·8	66·5
	Every third day	49·8	0·7	49·1	53·4
D	*Ad lib.*	54·0	1·0	53·0	76·1
	Every second day	51·2	1·2	50·0	65·8
	Every third day	49·9	1·0	48·9	52·2
E	*Ad lib.*	54·0	1·3	52·7	71·1
	Every second day	50·9	0·9	50·0	63·1
	Every third day	50·6	1·3	49·3	49·9
F	*Ad lib.*	54·0	1·2	52·8	70·2
	Every second day	51·1	1·0	50·1	62·9
	Every third day	50·1	0·7	49·4	47·8

sufficient of the previously prepared ration in an attempt to keep down the quantity of residues and to prevent any unnecessary selection of the chaff on offer. The withheld portions of the daily rations were weighed at the end of the trial and their dry matters were deducted from those of the previously weighed rations. Dry-matter determinations were also made on the weighed residues in the feeding boxes at the end of the trials, and in accordance with their analytical compositions, deductions were made from the constituents in the total ration on offer. The variations in the quantities of hay eaten therefore reflect appetite variations and do not indicate any deliberate restrictions imposed on the animals.

An analysis of variance of the average 6-day water consumptions in the different trial periods gave the results in Table 4, from which it is

TABLE 4. *Analysis of Variance in Average Water and Dry-matter Consumptions*

	Degrees of freedom	*Sums of squares**	*Mean squares**	*Variance ratio†*	*Significance level (P value)*
Water Consumption					
Between animals .	5	54·78	10·96	13·2	0·001
Between watering régimes . .	2	1555·57	777·79	939·8	0·001
Residual . .	10	8·28	0·83	..	..
Dry-matter Consumption					
Between animals .	5	2·49	0·50	5·0	0·05
Between watering régimes . .	2	39·79	19·89	198·3	0·001
Residual . .	10	1·00	0·10	..	..

* Rounded to two decimal places. † Rounded to one decimal place.

seen that both the differences between animals and between watering régimes were highly significant.

The data in Table 3 also showed that when kept indoors in digestibility crates and fed on hay, the oxen drank 12 per cent. less water when watered once every 48 hours than when allowed to drink as and when they wished, whilst when watered only once in every 72 hours, the reduction was 30·7 per cent. These reductions in water intake are comparable with those reported earlier [1], i.e. 10·8 and 31·7 per cent. respectively, when Zebu cattle were kept on similar watering régimes over a period of 31 weeks. These consumptions refer to housed animals consuming hay of 10–11 per cent. moisture content and are lower than would be required by the same cattle, exposed to the sun, or forced to walk long distances in a hot environment in search of food or water [1]. Equally they do not apply to similar animals feeding on green pastures or in humid environments [3].

Statistical analysis (Table 4) of the dry-matter intakes recorded in Table 3 indicates a significant difference (at the $P = 0{\cdot}05$ level) between the hay consumptions by the different animals, and a highly significant difference (at the $P = 0{\cdot}001$ level) in the quantities of hay eaten by the

same animal at differing frequencies of watering. It is apparent that for the oxen watered only once in every 48 or every 72 hours, the daily food consumptions fell respectively to 93·8 and 92·1 per cent. of the quantity eaten by the same animals when allowed to drink whenever they wished. Larsen *et al.* [2] similarly recorded a drop in dry-matter consumption by American milking cows watered once a day instead of once every 8 hours. More recently, Balch *et al.* [3] reported that dry dairy shorthorn cows in England, when restricted to a single daily watering limited in quantity to only 60 per cent. of their normal *ad lib.* intake, consumed

TABLE 5. *Digestibility Coefficients on Different Watering Régimes*

Watered	*Ox*	*Organic matter*	*Crude protein*	*Ether extract*	*Crude fibre*	*N-free extract*	*Total ash*	*Dry matter*
Ad lib.	A	47·9	58·2	10·5	49·2	46·0	32·0	44·7
	B	50·9	58·0	12·2	50·8	46·2	35·2	49·4
	C	49·1	58·4	11·2	48·0	46·9	27·2	46·9
	D	48·2	58·5	13·7	49·8	45·8	29·2	46·4
	E	46·3	57·9	13·9	48·7	43·0	30·4	44·8
	F	47·9	59·3	17·4	50·5	44·3	31·3	46·7
	Average	48·4	58·4	13·2	49·5	45·4	30·9	46·5
Every second day	A	48·8	59·6	19·0	52·5	44·4	28·9	46·9
	B	50·2	57·4	10·8	52·5	48·2	31·3	48·4
	C	48·0	57·8	9·2	52·7	43·4	25·6	45·9
	D	49·8	59·2	9·6	53·3	46·3	29·2	47·9
	E	48·6	57·4	8·3	52·8	44·5	29·1	47·5
	F	49·4	59·0	11·9	54·2	44·7	31·9	49·2
	Average	49·1	58·4	11·5	53·0	45·2	29·3	47·6
Every third day	A	48·9	57·1	10·7	52·2	45·8	27·6	46·9
	B	49·2	58·4	14·5	53·6	44·8	32·9	47·7
	C	48·2	57·8	17·3	52·5	43·7	25·2	46·7
	D	51·2	58·0	9·3	55·0	47·9	31·9	49·2
	E	49·3	57·0	14·9	52·9	45·9	30·4	47·5
	F	49·7	58·2	10·0	54·7	46·6	33·3	48·1
	Average	49·4	57·7	12·8	53·5	45·8	30·2	47·7

93·2 per cent. of the amount of lucerne hay eaten by the same animals under an *ad lib.* watering régime. The latter workers also observed alimentary adjustments, under conditions of restricted water intake, resulting in the maintenance of a normal water:dry matter ratio in the reticulo-rumen although the total weight of digesta therein had been reduced to 74·3 per cent. of the contents recorded in the *ad lib.* watering periods. The same authors recorded a decreased excretion of water in the urine and faeces during restrictions in water intake. Although the actual moisture excretory records of the present study are no longer available, there is no doubt that the faeces from animals on the restricted watering régime were much drier and harder than when the same animals were allowed an *ad lib.* water intake. In fact, with watering only once in 3 days, the faeces tended to form small balls and their alimentary movement was lubricated by means of an obvious mucous coating.

In Table 5 are summarized the digestibility coefficients for the various food components. No significant changes were observed in the digestibility coefficients, with the three rates of watering, for the dry matter, organic matter, crude protein, ether extract, or the nitrogen-free extract.

For the crude-fibre fraction, however, not only was a significant difference at the $P = 0{\cdot}05$ level recorded between animals but the digestibility coefficients for the different watering systems were significantly different at the $P = 0{\cdot}001$ level (Table 6). The average values were 49·5, 53·0, and 53·5 per cent. respectively, when watering *ad lib.* or only once in every 48 or every 72 hours. This increased fibre digestibility

TABLE 6. *Analysis of Variance in the Crude-fibre-digestibility Coefficients*

	Degrees of freedom	*Sums of squares**	*Mean square**	*Variance ratio†*	*Significance level*
Between animals .	5	10·82	2·16	5·3	0·05
Between watering régimes . .	2	56·06	28·03	68·9	0·001
Residual . .	10	4·07	2·41	..	..

* Rounded to two decimal places. † Rounded to one decimal place.

parallels the observations of Larsen *et al.* [2] and of Balch *et al.* [4] but, unlike the results of the former workers, there was no suggestion in this study of an increase in the digestibility of the crude-protein or the nitrogen-free-extract fractions with a reduction in the water consumption. In fact, although not significant, there was a general decrease in the

TABLE 7. *Calculated Nutritive Values of the Chaffed Hays Fed in the Different Periods*

	Water ad lib.		*Watered for 1 hour every 48 hours*		*Watered for 1 hour every 72 hours*	
Ox	*Digestible crude protein*	*Starch equivalent*	*Digestible crude protein*	*Starch equivalent*	*Digestible crude protein*	*Starch equivalent*
A	5·1	32·5	5·2	33·2	5·0	33·5
B	5·1	35·2	5·1	34·6	5·1	33·7
C	5·1	33·6	5·1	32·6	5·1	32·9
D	5·1	32·8	5·2	34·2	5·1	35·4
E	5·1	31·1	5·0	33·2	5·0	33·8
F	5·2	32·6	5·1	33·8	5·1	34·1
Average	5·1	33·0	5·1	33·6	5·1	33·9

crude-protein digestibility figures for the 3-day watering régime, which was possibly related to a need for an increased output of mucus to coat the faecal lumps of the drier excreta during this more rigorous watering system.

By using the digestibility coefficients in Table 5, in conjunction with the analyses of the rations fed (Table 2), the feeding values of the hay in the different trials have been calculated and the results are given in Table 7. In these calculations, and because all fodders were chaffed before feeding, Kellner's deduction of $0{\cdot}29 \times$ crude-fibre content has been employed for assessing the feeding value of the chaffed hay. Al-

though there was a slight increase in the average starch-equivalent value with increasingly severe water restriction, this difference was not statistically significant.

Calculation of the starch-equivalent intakes of the oxen when subsisting on the different levels of water restriction and an analysis of the results give the figures in Table 8. The respective calculated starch-equivalent intakes were 1·45, 1·39, and 1·38 kg. with the decreasing frequencies of watering and although the analysis of variance (Table 8) indicated that the differences in these energy intakes were significant at the $P = 0{\cdot}05$ level, further analysis indicated that this level of significance was achieved only for the comparison between the *ad lib.* and the once-every-three-days watering systems. The figures for the 2-daily watering system did not differ significantly from those for the other watering régimes. These results were thus in line with those of Balch

TABLE 8. *Analysis of Variance in Starch-equivalent and Digestible-Crude-Protein Intakes*

	Degrees of freedom	*Sums of squares**	*Mean squares**	*Variance ratio†*	*Significance level (P value)*
Starch Equivalent					
Between animals .	5	14484	2897	1·3	N.S.
Between watering régimes . .	2	19683	9842	4·4	0·05
Residual . .	10	22272	2227	..	..
Digestible Crude Protein					
Between animals .	5	101	20	3·4	N.S.
Between watering régimes . .	2.	1100	550	91·4	0·001
Residual . .	10	60	6	..	..

* Rounded to nearest unit. † Rounded to one decimal place.

et al. [4] who found no reduction in the available starch equivalent when the daily water consumption was reduced to 60 per cent. of the *ad lib.* intake given only once during each day. The more extreme restriction, in the present series, to watering only once in 72 hours indicates that local Zebu cattle on an *ad lib.* ration in the drier areas obtain a lower daily energy intake as a direct consequence of water shortage, and that unless unavoidable, such severe restrictions should not be practised. When, as usually happens, the water shortage is accompanied by an inadequate dry-matter intake or the consumption of bulky fodders of low feeding value, much more serious consequences can be expected.

The average daily digestible-protein intakes were 212, 199, and 193 gm. respectively, for *ad lib.* watering and when watered once in 48 or 72 hours. An analysis of variance of these figures (Table 8) showed no statistical significance in the differences between individual oxen but highly significant differences (at the $P = 0{\cdot}001$ level) between the watering régimes.

Discussion

Because the productive efficiency of Zebu cattle, under African management conditions in East Africa, is often of a low order, it is desirable to determine the relative importance of such contributing factors as management, nutrition, and climate in areas where disease is controlled either naturally or by veterinary aid. This paper seeks to determine the consequences of one of the environmental factors operating in arid and semi-arid areas, namely the influence of water shortages and long intervals between drinkings on digestive ability.

In the more arid areas, the African husbandman has long been accustomed to the consequences of seasonal undernutrition and, in accordance therewith, has developed a traditional management procedure which seeks to apportion the activities of his stock so as to balance the time wasted, from a grazing point of view, against the imperative need to walk them long distances to water. The consequences, when cattle are existing on a dry-hay ration, of watering for 1 hour every second or every third day have been examined. It appears that such severe water restrictions reduce appetite and food intake, even when an adequate quantity is on offer, but that under such conditions the digestibility of the crude-fibre fraction is increased. Whereas this increased digestibility adequately compensates for the lower dry-matter intake, when watering is not too infrequent, there are limits beyond which this compensatory action cannot be stretched. The results show conclusively that the starch-equivalent intakes, on a 3-day watering régime, were significantly lower than when water was constantly available. The restriction in food intake, caused by this infrequency of watering, outweighed any chance of the diminished intake being compensated by a proportionately greater digestibility of the crude fibre fraction. The practical consequences of this observation suggest that water-conservation measures in the more arid areas should, where feasible, attempt to provide storage reservoirs so that the cattle never need to subsist for longer periods than 48 hours without drinking. This should not of course be the final objective, but even such a limited improvement would remove the worst features of the present system and contribute importantly to livestock efficiency.

With restricted watering, the quantity of digestible crude protein apparently available to the animals was significantly reduced. While this may well be a direct consequence of the infrequency of watering, it is not in line with the results of American and British workers for less severe restrictions on water intake. In fact, it may be that the apparent reduction in digestible-crude-protein intake is an artefact consequent on the need of the cattle to excrete larger quantities of mucus to lubricate the movement of the dry excreta through the last sections of the alimentary canal.

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SOME MANURING EXPERIMENTS ON OIL PALM IN AFRICA

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Summary

Results from ten manuring experiments on oil palm in Nigeria, Cameroons, and the Belgian Congo are presented. Highly economic returns from the use of potassium were established in most cases, with smaller and more variable responses to phosphorus, and only uncertain or uneconomic ones to nitrogen. Calcium and magnesium limestone and magnesium sulphate were tested without significant response. Differences in response were shown between two soil types and between Lisombe and Deli palms. The differences could be related to the analysis of the soils for total P and K, although the conventional estimates of soluble or exchangeable fractions failed to show any clear relationship.

Possible interference from edge effects was taken into account in the design and recording of the experiments and these effects are shown to develop in a way clearly due to poaching of fertilizers by palm roots crossing plot boundaries. This necessitated important corrections in the later years.

In addition to a definite annual yield cycle dependent on rain seasons, the data revealed marked cycles in yield with three- to five-year periods, relatively large amplitudes, and complicated phase relationships which are probably influenced by the fertilizers. If this is not taken account of it can render the conventional interpretation of short-term results obscure and even misleading, and it produces unusual features in the analysis of variance.

THE experiments to be described were initiated at the time of the West African Commission 1938–9 appointed by the Leverhulme Trust, of which the late Dr. E. M. Crowther was a member. They were planned by him and started in 1940 with all facilities provided by the Unilever organization, covering ten sites, two varieties of palm, and both mature and immature stands of palms. During his lifetime Dr. Crowther guided the experiments and wrote reports for private circulation, and it is as a tribute to him that a complete reworking of the data has been undertaken for this presentation of the results. They cover the records up to 1954 when the older stands were getting near the end of their economic life and all the salient features of the experiments were fully established.

Description of Experiments

In all cases the well-known 27-plot design of experiment was followed in which the three elements N, P, and K are tested at two rates of application, the plots showing all combinations of the levels (0, 1, 2). In one case (Kangala, Belgian Congo) the design was elaborated to 81 plots to include tests of Ca (high-calcium limestone) and Mg (high-magnesium limestone), each at one rate. In another case (Cowan, Nigeria) three similar experiments were combined in 1950 to include a test of Mg as magnesium sulphate at three levels (0, 1, 4). The plots were in continuous compact blocks of uniform planting marked by weeded separating paths, and each was arranged to consist of 6×8 rows

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of palms, or 48 planting points. The spacing is 30 feet triangular giving about 56 palms to the acre. In order to detect possible boundary effects the 24 palms forming the boundary rows were always recorded separately from the 24 inside palms, which later may therefore be regarded as in some sense protected. The records were returned as annual weight of fruit bunches, number of bunches, and number of fruiting palms per group of 24 palms. These had been compiled from daily harvests of individual palms, the produce being weighed in the field and entered weekly. The units throughout this paper are kilogrammes of fruit bunches per planting point (loosely 'per palm'). The capitals N, P, K, &c., refer to the nutrient elements, and when an apostrophe is added this symbol represents their effects (being the difference between means of plots with and without that treatment); thus K_1', K_2' represent the potassium effect at single and double level respectively, and K_m' the mean of these. The usual convention is followed of indicating the statistical significance of a figure by one star for $P = 0{\cdot}05$ and two stars for $P = 0{\cdot}01$.

Site data. Nine 27-plot experiments were laid out, 5 at Ndian estate (Cameroons) and 4 at Cowan estate (Benin, Nigeria). Another experiment, of 81 plots, was at Kangala, Belgian Congo. At Ndian two soil types were distinguished, one a brown clay with much laterite gravel derived from basalt (Experiments 2 and 4) and the other a pale coarse sand derived from quartzose gneiss (Experiments 1, 3, and 5). The basalt consists of large loose boulders with soil interspersed to considerable depth, very free-draining. The gravel is not confined to normal horizons but is much in evidence on the surface. At Cowan the soil is sandy in each case, the derivation being deep Tertiary sand. The Kangala soil is also described as sandy, and is considered to be a good one by local standards. In Table 1 are given the dates of planting and type of palm together with the salient features of soil analyses carried out on composite samples taken in 1949 from all P_0K_0 plots. We are indebted to R. G. Warren for these analyses. The soils exhibit the acidity to be expected in the rain tropics, where experience indicates that ground rock phosphate will be an active fertilizer.

The figures for soluble P were obtained by the 0·5 normal acetic-acid method and the exchangeable bases by extraction with ammonium acetate and spectrographic determination. All these are low and are not clearly related to the experimental responses which are to be discussed. The figures for total P and total K, however, do have a very clear relationship to the experimental findings. At Ndian the sands are marked by low total P and the gravels by low total K, while the Cowan sands are low in both elements, and the outstanding responses to P and K fertilizers correspond inversely to the soil content, as would be expected. The Kangala figures are similar to Cowan but responses there were not nearly so good.

All sites maintain a good ground cover, mostly of wild species but usually containing a proportion of the creeping legumes originally sown. Slashing is needed once or twice a year. Boundaries of plots are marked by weeded paths but the remaining access paths and rings round the

TABLE 1. *Site data*

Experiment no.		*Planting date*	*Variety Lisombe or Deli*	*Soil Analysis*										
					pH	*Stones over 2 mm.; % of fine earth*	*P*		*K*	*Exchangeable cations*				
							Total	*sol.*	*Total*	*K*	*Na*	*Ca*	*Mg*	*Mn*
							mg./100 g.							*p.p.m.*
Ndian sands	1	1933	L	Soil 0–25 cm.	4·6	32	25	0·07	400	3	4	11	2	3
				Sub. 25–60 cm.	4·7	46	26	0·00	410					
	3	1933	L	Soil	4·7	18	20	0·03	620	5	4	12	2	3
				Sub.	4·8	47	19	0·00	610					
	5	1930	D	Soil	4·4	19	15	0·03	1,110	3	5	9	1	2
				Sub.	4·8	50	23	0·01	1,050					
Ndian gravels	2	1930	L	Soil	4·4	107	250	0·01	97	3	3	16	1	3
				Sub.	4·6	66	246	0·00	100					
	4	1930	D	Soil	4·5	91	257	0·05	110	3	3	19	1	2
				Sub.	4·7	107	254	0·03	97					
Cowan sands	1	1936	L	Soil 0–25 cm.	4·6		16	0·10	41	2	3	34	1	2
				Sub. 25–100 cm.	4·4		15	0·00	35					
	2	1936	L	Soil	4·9		12	0·10	30	1	3	20	1	5
				Sub.	4·6		17	0·07	33					
	3	1936	L	Soil	4·8		14	0·19	31	3	4	31	1	3
				Sub.	4·7		14	0·00	26					
	4	1940	L	Soil	5·0		17	0·11	31	3	3	25	2	10
				Sub.	4·5		20	0·00	37					
Kangala		1932	Local strain	Soil	4·9	no stones	14	0·06	35	2	3	22	1	9
				Sub.	4·3		23	..	38					

palms carry closely cut grass (Paspalum). There are no striking visual contrasts between plots either in the palms or ground cover.

History of fertilizer application. In Table 2 are given the rates of fertilizer application each year. The time of application was always in the dry season, generally January or February, but if the date was a little earlier (that is, late in the previous calendar year) the application is credited to the first full year in the table. At Ndian the last dressing was 1951, because the end of the economic life of the palms was approaching, but recording has been continued. Nine plots comprising one block are assigned for treatment in one day's work. The fertilizers are not mixed

TABLE 2. *Fertilizer applications, Kg. material per palm (for single rate)*

	Ndian			*Cowan*				*Kangala*				
	N	P	K	N	P	K	Mg•	N	P	K	Ca	Mg+
1941	0·75	0·75	0·5•	0·5	0·5	0·33•	..	0·75	0·75	0·5•	5·0	5·0
2	0·75	0·75	..	..	..	..	..	0·75	0·75	0·5•	5·0	5·0
3	..	..	..	..	..	..	..	0·75	0·75	..	5·0	5·0
4	0·75	0·75	0·5+	0·75	0·75	..	..	0·75	0·75	..	5·0	5·0
5	..	..	..	..	..	..	..	0·75	0·75	0·5•	5·0	..
6	0·75	0·75	0·5+	0·75	0·75	0·5+	..	1·5	1·5	..	10·0	..
7	1·5	1·5	1·0+	1·5	1·5	1·0+	..	1·5	..	1·0•	10·0	10·0
8	1·5	1·5	1·0+	1·5	1·5	1·0+	..	1·5	1·5	1·0•	10·0	10·0
9	1·5	1·5	1·0+	1·5	1·5	1·0•	..	1·5	1·5	1·0•	10·0	10·0
50	1·5	1·5	1·0+	1·5	1·5	1·0•	0·25	..	..	..	..	..
1	1·5	1·5	1·0+	1·5	1·5	1·0•	0·25	..	..	..	..	..
2	..	..	..	1·5	1·5	1·0•	0·25	..	..	..	..	..
3	..	..	..	1·5	1·5	1·0•	0·25	..	..	..	..	..
4	..	..	..	1·5	1·5	1·0•	0·25	..	..	..	..	..

N as sulphate of ammonia.
P as ground rock phosphate (North African).
K• as sulphate.
K+ as chloride.
Mg• as sulphate.
Mg+ as high-magnesium limestone.
Ca as high-calcium limestone.

but taken into the field in separate bags of the weighed amounts for one plot, and measured out there for each palm from a packing case. Application is by broadcasting in a ring outside the weeded area around the stem, but within the spread of the fronds, followed in earlier years by light hoeing to 2 or 3 inches depth.

The history falls into two periods: (1) 1941–6 with intermittent application at lower basic rates, (2) 1947 onwards with regular annual dressings at double the former basic rates, amounting on the average to three times the previous intensity for N and P and four times for K.

Plot size. The best size of plot is determined primarily by the variability of the individual palms, for the genetic differences far outweigh soil variation. A most important feature to be noted is that annual yields of individual palms and of plots do not vary at random, but are linked by definite cycles of three or four years duration. Annual records therefore suffer from large errors which diminish when the longer period of a complete cycle is taken. Thus the standard errors of the yearly plot records of No. 2 Ndian for 1941–4 were 8·9, 8·4, 10·1, and 7·5 per cent.

of the mean, but this was reduced to 5·9 per cent. on averaging the four years.

Frequency tables were examined for yields of individual palms in Nos. 1 and 2 Ndian for 1941–4. These showed a group of very low yielders (probably supplies) distinct from the main group and comprising about 14 per cent. of the whole. The better half of the palms contributed just over two-thirds of the yield. Three examinations (Nos. 1 and 2 Ndian, 48 palms, 4 years and No. 2 Cowan, 24 palms, 13 years) gave values for the standard error per palm within plots 53·6 and 49·9 per cent. of the mean for the 4-year periods and 48·3 per cent. for the 13-year period. The plot experimental errors for the same three sets of data were 8·4, 5·9, and 11·7 per cent. of the mean. A combination of 48 palms as a plot unit therefore reduces the variance due to palms to a value reasonably commensurate with the experimental error to be expected from most sites.

Competition between palms is always evidenced by the inordinately slow growth of young supplies planted among older palms. Strong individuals may therefore win advantages at the expense of weak neighbours, which increases the error per palm but provides compensations when combining groups. Some evidence of this is suggested in No. 2 Ndian, which has a falling yield and probably high competition.

Experimental Results

Main effects and interactions. A condensed and very general outline of the results is given in Table 3 as the average at the two estates for the

TABLE 3. *Effects as Average of Two Levels of Application, compared with Costs (1949 relationships of values)*

	Mean Annual Values, kg. fruit per palm					
	Low-manuring period			*High-manuring period*		
	1941–6			*1947–51*		
		Response			*Response*	
Locality	*Cost*	*Sand*	*Gravel*	*Cost*	*Sand*	*Gravel*
Ndian 5 expts.	N 2·7	1·7	1·5	8·1	3·4	3·7
	P 1·0	1·2	0·5	2·9	6·1	0·5
	K 1·4	0·9	2·0	5·7	3·7	12·0
	1941–6			*1947–54*		
Cowan 3 expts.	N 1·8	3·4		8·1	4·0	
	P 0·6	−1·0		2·9	1·7	
	K 0·8	4·0		5·7	14·6	

two periods of low and of high rates of application. To assist judgement on the economic question approximate costs are given, in the same units, calculated for the relationships of values existing in 1949. The cost of N is high and the responses from continued treatment inadequate, but since most responses came early it may be that limited applications sometimes

TABLE 4. *Main Effects and Interactions. Forty-eight palms. Kg. fruit bunches per palm*†

Period	*Experiment*	*Mean yield*	N_1'	N_2'	P_1'	P_2'	K_1'	K_2'	*s.e.*	N_2' P_2'	N_2' K_2'	P_2' K_2'	*s.e.*
			A. *Mean annual production*										
1940–54	Ndian sand 1	54·9	3·7	5·2*	1·5	1·9	4·3	3·0	±2·08	1·9	−3·2	3·1	±2·55
	Ndian sand 3	57·7	2·3	4·8*	6·4**	2·9	1·8	2·2	±1·96	−3·6	−1·5	−2·1	±2·41
	Ndian gravel 5	64·1	−1·8	−1·5	4·7**	2·5	3·9*	0·8	±1·53	5·0*	−1·3	−3·1	±1·88
	Ndian gravel 2	61·7	1·1	1·3	−4·5**	−1·2	9·5**	9·1**	±1·31	−1·3	−0·8	−2·4	±1·62
	Ndian gravel 4	54·9	1·9	3·0	2·3	5·5*	6·9**	7·8**	±2·19	1·1	0·5	1·8	±2·69
1942–54	Cowan sand 1	51·9	0·9	5·6*	−0·8	−1·1	4·1	7·6**	±2·55	3·3	5·1	2·8	±3·12
	Cowan sand 2	58·1	0·6	2·0	2·1	2·5	7·5*	9·2**	±2·74	3·6	3·2	2·5	±3·34
	Cowan sand 3	58·2	2·4	6·0**	1·6	2·9	9·4**	12·2**	±1·66	−0·8	−3·5	4·6*	±2·03
1946–54	Cowan sand 4	40·7	2·0	4·0	−0·3	−2·1	4·7*	6·2**	±2·02	−1·8	−3·1	1·2	±2·48
1940–51	Kangala	70·2	2·2	2·5	−0·6	0·5	−1·9	2·6*	±1·27	−1·0	1·8	−1·5	±1·56
			B. *Mean annual change*										
1940–54	Ndian sand 1	1·09	−0·60*	−0·07	0·57*	0·28	0·08	−0·02	±0·239	0·14	−0·24	0·25	±0·293
	Ndian sand 3	1·05	−0·03	0·23	0·36	0·37	0·64**	0·42*	±0·184	0·27	−0·25	0·31	±0·224
	Ndian gravel 5	0·77	0·22	0·03	0·80**	0·85**	0·74**	0·86**	±0·179	−0·11	0·08	0·32	±0·218
	Ndian gravel 2	−0·42	0·13	−0·06	−0·30	−0·28	0·78**	1·00**	±0·194	0·13	0·62*	0·10	±0·236
	Ndian gravel 4	0·35	0·02	0·16	0·09	0·29	1·43**	1·75**	±0·232	0·31	−0·29	0·08	±0·284
1942–54	Cowan sand 1	2·15	−0·15	0·12	0·36	0·24	0·83**	1·31**	±0·239	0·11	0·19	0·01	±0·292
	Cowan sand 2	2·69	0·12	−0·04	0·52	0·26	1·23**	1·54**	±0·321	0·40	0·20	0·09	±0·393
	Cowan sand 3	2·15	−0·03	0·29	0·22	0·67*	1·15**	1·95**	±0·286	0·48	−0·57	−0·17	±0·351
1946–54	Cowan sand 4	2·95	−0·17	0·27	−0·09	−0·46*	0·77**	1·14**	±0·199	−0·27	−0·27	−0·12	±0·245
1940–51	Kangala	−0·69	−0·15	−0·01	0·14	0·19	0·42*	0·72**	±0·164	−0·15	0·02	0·23	±0·201

† A factor × 56 transforms to kg. per acre.

have economically good effects. The general aspect of lush covers and perpetual rotting-down of debris suggests that nitrogen deficiency was not a special characteristic of any site. The cost of P is low and with the variable results it becomes a matter of carefully selecting the occasions for its use. K had outstanding effects of high economic importance, even for the very low rates given at Cowan in the early period, and calls for very little discrimination as to its use on any of these sites.

In Table 4 is given a complete summary of the experimental results, taking simply the full period and plots of forty-eight palms. The measures taken are: A, the mean annual production of fruit; and B, the mean

TABLE 5. *Two-way Tables reduced to Mean of Two Levels of Application and referred to relevant controls as 100. Seven years' total production 1947–53. Twenty-four inside palms*

NDIAN									COWAN								
Expt. no.		*Po*	*Pm*	*Ko*	*Km*		*Ko*	*Km*	*Expt. no.*		*Po*	*Pm*	*Ko*	*Km*		*Ko*	*Km*
1	No	100	119	100	120	Po	100	108	1	No	100	104	100	129	Po	100	125
	Nm	114	125	122	122	Pm	114	120		Nm	113	117	114	145	Pm	95	127
3	No	100	107	100	106	Po	100	110	2	No	100	104	100	121	Po	100	118
	Nm	103	114	105	112	Pm	112	119		Nm	104	109	101	129	Pm	98	127
5	No	100	114	100	102	Po	100	116	3	No	100	96	100	141	Po	100	124
	Nm	99	112	95	102	Pm	125	126		Nm	104	105	119	133	Pm	96	124
2	No	100	88	100	124	Po	100	144	4	No	100	99	100	108	Po	100	107
	Nm	98	93	98	130	Pm	104	130		Nm	99	104	97	114	Pm	97	114
4	No	100	105	100	138	Po	100	111									
	Nm	104	109	103	142	Pm	83	126									

Kangala 1944–51. Forty-eight palms

	Po	*Pm*	*Ko*	*Km*		*Ko*	*Km*		*O*	*Ca*	*Mg*		*O*	*Ca*	*Mg*		*O*	*Ca*	*Mg*
No	100	102	100	100	Po	100	102	No	100	97	97	Po	100	97	97	Ko	100	97	98
Nm	105	105	102	105	Pm	101	102	Nm	101	102	102	Pm	98	99	99	Km	100	100	100

annual change in production (linear regression). The interaction given in this table is that at the double level but to assist examination more closely two-way tables of 24-palm plots for the high-manuring period are set out separately in Table 5, the sections being referred in this case to percentages of the relevant controls. Means have been taken of the two levels to economize space and improve accuracy. This seems justified by the general similarity of results from the single and double levels. The entries in such two-way tables have different errors, being derived as to the controls from three plots and as to the other entries from six or from twelve plots. They serve, however, in view of the support which one experiment gives to another, to bring out some important features.

Fig. 1 gives a conspectus of the development of the main effects on yield over the years for individual experiments, based on three-year running means. Cowan 4 is omitted because it was immature for a considerable part of the time, and Kangala because effects were so slight.

The inside half-plots have been used for this diagram. The first curve in each case is the history of the mean yields, enabling a discrimination to be made by comparison of the trends between younger or more progressive stands and those which have reached a steadier level, or which represent lower-fertility sites. N_m', P_m', and K_m' are plotted to the same

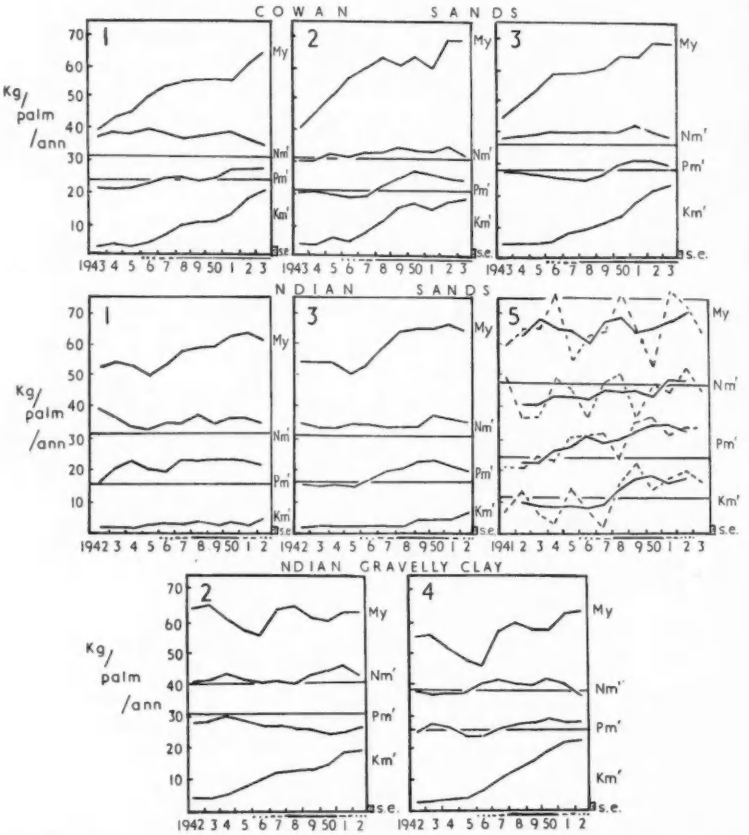


FIG. 1. Mean yield and mean effects by years. (Smoothed by running mean of three-year periods.) Incidence of high-rate manuring indicated thus $\frac{3}{}$ $\frac{2}{- -}$ $\frac{1}{\cdots}$ years out of three.

scale as the mean yields, each curve having its own zero axis shifted arbitrarily for convenience of spacing. An approximate value of the standard error which applies to the responses plotted is shown by the small shaded pillar at the bottom right-hand corner of each diagram. In the case of Ndian No. 5, chosen as the best example, a broken line shows how the annual values follow a regular rhythm and reveals the reason for using the device of the three-year running mean. The time-incidence of

the treatments is blurred by such a device, but this is not very important for the slow changes represented.

Discussion and Conclusions

Cowan sands. Much of the land here had been previously farmed. The water-table is high in the rainy season, but drainage is good and (especially in No. 4) leads to a low water-table in the dry season. The regressions during the period of high rates of manuring show P and K to have had good effects on yield, both highly remunerative, but there are anomalies in the early period as well as considerable influence from the first choice of plots on the figures for total produce. On the face value of the early period of the three Cowan experiments, as shown in Figure 1, two start off with apparent good N effects and all show negative P effects and positive K effects. Of these only K' is supported by later events. P might at first deflect energy to root development, and N may at first stimulate leaf emergence with increased rate of appearance of bunches, but on the whole the suggestion contained here that N has a quick but not a cumulative effect and P only a slow effect cannot be regarded as clearly proved. The results measured by mean annual change probably best repay attention as it is in the nature of the case for the palms to integrate the results of a succession of applications, and the method of calculation is likely to lessen variation due to the permanent genetic or soil differences between plots.

Table 5 shows a small but consistent depressive effect of P in the absence of K at Cowan. Although this interaction only reaches significance level in No. 3 (Table 4 A), it was to be noticed that plots with double P and no other fertilizer were consistently low, suggesting that phosphate should not be used alone nor too profusely on this soil. Later observations on wilt disease showed an increased incidence where P had been given without K in Nos. 1 and 4. It should also be remembered that other elements accompany the P treatment and may be exerting unrecognized influences.

There were no effects apparent from the magnesium treatment, started in 1950 on experiments 1, 2, and 3 by confounding this treatment with a high-order P × K × rates interaction. Mg-deficiency symptoms are now (from local investigations) clearly identifiable in 'orange frond' and these symptoms are beginning to appear on plots at Ndian, though not at Cowan. It still remains to be shown how far these symptoms can develop before yield is seriously affected.

Experiment No. 4 is characterized by the fact that manuring started soon after planting (1940). The soil is coarser sand with less clay than the others and a much darker red colour. When yields began in 1946 it was clear that there had been no marked effects in hastening maturity. P has had a negative cumulative effect and K a positive one, though not nearly as large as in the other experiments. It was to be noted that the mean yield made very slow progress in this experiment up to 1953 and it seems probable that some limiting factor, not reached by the treatments, was in operation.

The tables of analysis of variance of these experiments are remarkable

for the number of subnormal values, some of them of high significance. It has become clear that there are rhythmic movements of yield, discussed in later paragraphs, which give rise to an inflated estimate of error if they are treated in conventional examination of annual results as though they were random. It follows that in suitable circumstances there is much opportunity for compensations to arise to reduce items of variance, and, if the time-positions of yield maxima and minima are affected by treatments, then the reduced variance may be associated with treatment in complex ways.

Table 6 illustrates differing ways of calculating the regressions of the three experiments combined as eighty-one plots, over the period of high rates 1947–53.

TABLE 6. *Methods of Calculation compared, Cowan eighty-one plots. Mean annual change during high-manuring period 1947–53 kg./palm/annum*

	N_1'	N_2'	P_1'	P_2'	K_1'	K_2'	*s.e.*	*t values* K_1' K_2'
Using 48-palm plots . .	0·24	0·32	0·45	1·10**	1·27**	1·93**	±0·336	3·8 5·7
,, 24 ,, . .	0·18	−0·26	0·88*	0·84	2·04**	2·75**	±0·444	4·6 6·2
24 palms smoothed by 3-year running mean	0·01	−0·41	0·85**	0·83**	1·88**	2·42**	±0·309	6·1 7·8

Although the use of forty-eight palms gave, as expected, a lower error than limiting the plots to twenty-four protected palms, these latter achieve a higher significance of the prominent K' because its magnitude is enhanced. In the third line a smoothing of three-year cyclic movements has been secured by using annual values of a three-year running mean for each plot. In spite of the fact that such treatment in general decreases the efficiency, it has in this case increased it considerably, halving the error variance, which is an improvement afforded in general in field experiments when the number of plots is doubled. In this last calculation the regression of P_m' in the presence of K was 1·04* ±0·326 kg. per palm per annum[2]. This falls to 0·45 kg. per palm per annum[2] in the absence of K, and does not achieve significance.

Ndian sands. The three experiments on this soil include one (No. 5) with the distinctive Deli palm. This variety was produced by selection in the more sunny climate of Sumatra and does not generally look so well as the local Lisombe. No. 1 is described as having better drainage than Nos. 3 and 5, while the colour of No. 5 is reddish and of No. 3 grey. The early apparent positive effect of N on Nos. 1 and 3 is reminiscent of Cowan, with no increase from continued treatment. The negative N' in No. 5 in the second year had two-star significance, but this must obviously be regarded as largely an adventitious minimum in the cyclic movements. P has had consistently good effects on this soil, and may be regarded as a main requirement. K has had smaller effects in these experiments than the others, which is consonant with the higher analysis for total K (Table 1). They are barely economical in the cases of Nos. 1 and 3.

Ndian gravels. K has had very distinct effects on this soil while N'

does not achieve conventional significance. P' has opposite signs for the two experiments. In the case of Lisombe palm, No. 2, there is a significant N × K interaction on the regressions but as the sign changes in the case of the average production it can have no major importance. This interaction reached two-star significance in the regressions of bunch numbers, in a table showing no other marked feature. This may probably be ascribed to change in phase between the regular rhythms, but in any case it well illustrates the unusual nature of the data which oil palms give. In No. 4 the interactions of Table 5 show a positive P × K interaction which is significant. The form it takes is a negative influence of P when applied without K, but this is not repeated by the Lisombe experiment on similar soil.

The contrasts between soil types and palm variety are brought out in Table 7. If Nos. 1 and 3 are averaged we have for comparison the responses of each kind of palm on each kind of soil. The differences have been calculated on the regressions for the full period. Deli palm has given better responses than Lisombe for both P and K, while gravel soil

TABLE 7. *Response Differences at Ndian: Lisombe palm* v. *Deli, and sand* v. *gravel*

Mean annual change 1940–54, kg./palm

Difference	N_1'	N_2'	P_1'	P_2'	K_1'	K_2'	*s.e.*		P_0K_0 plots D	P_0K_0 plots L
Deli minus Lisombe	0·22	0·08	0·36	−0·55*	0·52*	0·71**	±0·206	sand	−0·24	0·81
Gravel minus sand	0·12	0·00	−0·74**	−0·58*	0·56*	0·85**	±0·206	gravel	−0·67	−0·65

responded better than sand to K and sand responded better to P than gravel. The mean regressions for P_0K_0 plots, used to indicate the nature of the sites, show how poor the gravels are. The Lisombe experiments appear to be the better sites on the sand, but the palms in this case are three years younger.

Kangala. The Kangala experiment proved an excellent one for accuracy, but only K gave significant positive results, the P effect being positive but too small for clear proof. Table 5 shows that limestone without interaction with other fertilizer was in all cases slightly depressive. The palms were planted in 1932 and so were fully mature when manuring started. Though the yield level is higher than other experiments the mean regression has a substantial negative value. This suggests that there should have been room for improvement by maintenance of yield and that the treatments have not overcome some unidentified limiting factor.

Rates of application. The rates of application used from 1947 onward appear from the narrow difference between the responses at two levels to have been very liberal in relation to the needs of the palms. From the data considered by Wilbaux [1] it may be estimated that the unit levels per palm of 1·5 kg. sulphate of ammonia, 1·5 kg. rock phosphate, and 1·0 kg. potassium chloride bear the following approximate relationships to the amounts of N, P, and K removed by the fruit; N nearly equivalent,

P nine times, K more than twice. The double level of K, allowing some five times the requirements of the fruit, probably would leave the palms little to seek elsewhere if absorbed without large losses. The Cowan mean annual responses to K over the high-manuring period 1947–54 measured by eighty-one 24-palm plots were 12·8 kg. for the single level with an equivalent expenditure of 3·8 (i.e. a return of over three times the cost), but for the addition of the second level this was increased only by 3·6 kg. which does not quite repay the added cost. The reckoning has similar relationships if the periods be varied. The optimum dressing was not very far from the single level of the high-manuring period for Cowan sands and Ndian gravels. However, the guidance afforded by the experiments must be liberally interpreted since a higher efficiency in the practical use of fertilizers is likely to be secured. In addition to deciding the best quantities there is the question of periods between application where rainfall and soil type suggest that leaching of soluble fertilizers may be serious, and where palms may go through seasonal changes in receptiveness. The very wide margin of profit provided by the use of K would also incline judgement of treatment toward the liberal side, because the lost opportunity represented by under-dosage is much more important than the small diminution in gain represented by moderate over-dosage. The early good results, especially at Cowan, suggest that low dosage can still be relied upon to give high proportional results, so that in the case of limited supplies they should be well spread to get the best return.

Edge effects. Palms along the edges of plots have the opportunity by root-spread to gain some undesigned advantage when more effective treatments have been used on neighbouring plots. They also suffer greater hazards, represented in this case by weeded and well-trodden paths. The first influence, which we may term 'poaching', will be manifest as a decay of integrity of the measurements of results, shown according to the effectiveness of the treatment concerned and then mainly on the control plots, where the intention to starve has to some extent failed.

Tables 8 and 9 give the outlines of this poaching story. Table 8 gives the regression coefficients of the annual differences between the measures of the chief plot groupings when assessed separately from outside and inside palms. The significant figures that appear are all concerned with the control plots, and have the sense that outside palms have been securing some cumulative benefit over the inside ones. The figures also conform in magnitude to the relative effectiveness of the fertilizers, viz. highly significant for K, less so for P, and not significant for N. The transfer of treatments across boundaries is, of course, only fractional, and while it has these marked effects on starved plots on the positive side of the account, it is seen that in the rest of the table the effects of losses from treated plots (or the minus side of the account) are negligible. Table 9 provides another way of presenting the facts, designed to give an estimate of the correction to be applied to K_m'. The ratio of the inside and outside measures of K_m' have been taken for triennial periods. Since each measure represents by definition the same thing from two distinct evaluations of the plots, the ratio (in the absence of interference) should hover near

unity. Neglecting the first period at Cowan, where values are smaller than the error and the ratio is meaningless, it is seen that the ratio steadily grows until in the last years it has nearly reached 2. Actually in 1953 it did exceed 2 at Cowan, giving a correction factor of 4/3 to be applied to the conventional 48-palm measure of K_m'. The older palms at Ndian were the earliest to develop the K effect and much the earliest, by virtue of their greater root-range, to begin poaching.

TABLE 8. *Comparison between Inside and Outside Palm Yields, expressed as a linear regression of the difference on time*

Difference (outside minus inside): Mean annual change. Kg./planting point/annum.

Estate	*Treatment*	*Rate*					
		None		*Single*		*Double*	
Ndian 1941–53 .	N	0·05	±0·13	0·11	±0·14	0·10	±0·10
Mean 5 expts. .	P	0·21	±0·13	0·11	±0·15	−0·04	±0·10
(135 plots) . .	K	0·33**	±0·07	0·00	±0·15	−0·05	±0·10
Cowan 1943–53 .	N	−0·06	±0·27	−0·01	±0·16	−0·30	±0·21
Mean 3 expts. .	P	0·23*	±0·11	−0·00	±0·20	0·01	±0·20
(81 plots) . .	K	0·64**	±0·12	−0·26	±0·23	−0·09	±0·23

Edge effects appear to be on the whole detrimental. As an instance it can be stated that the mean linear regression at Cowan (Expts. 1, 2, and 3) during the period of high manuring (1947–53) was nearly twice as large for the inside palms as for the outside. The difference between them was inside minus outside = 0·62±0·28 kg./palm/annum[2]. This result suggests that some sacrifice has been made by clearing paths for boundaries and their consequent consolidation.

TABLE 9. *Triennial ratios of K_m' inside/K_m' outside*

		1942–4	*1945–7*	*1948–50*	*1951–3*
Ndian gravels: K_m'	48 palms	4·6	6·7	11·0	15·6 kg./palm
(54 plots)	ratio 24 in/24 out	0·87	1·67	1·93	1·97
Cowan sands: K_m'	48 palms	2·6	4·1	10·0	14·1 kg./palm
(81 plots)	ratio 24 in/24 out	(0·27)	1·18	1·58	1·88

It may be suggested for consideration that an effective and economical substitute for guard rows might be found by cutting trenches along plot boundaries, keeping them filled but opening and refilling them once a year to check root travel.

Effects on disease. Parallel with the yield benefits there were improvements in the health of the palms. In 1951 a disease census was carried out on the Cowan experiments with the results summarized in Table 10. The incidence of diseased palms was high, but was consistently reduced by over one-third by the application of K at the double level.

Partition of effects between classes of palm. The good effect of K on

palms of low performance implies that a similar economic return may be made by all classes of palm. In Table 11 the thirteen-year individual totals for the 24 inside palms of each plot of No. 2 Cowan have been partitioned between classes by taking groups of five palms of each plot graded according to yield. The fifth and last group then contained only four palms, including gaps. Partitioned in this way the absolute values

TABLE 10. *Cowan Diseases Census*

Number of diseased palms (including deaths) per 100 palms planted

Experiment	*1*	*2*	*3*	*4*
Mean	*31·71*	*17·28*	*29·55*	*18·52*
N_1' . .	−4·6	0·7	−1·4	0·6
N_2' . .	−6·5*	4·0	−3·8	−1·4
P_1' . .	2·6	−3·8	4·1	−1·6
P_2' . .	1·6	−0·7	−3·0	−3·2
K_1' . .	−8·4*	−6·5	−8·5*	1·2
K_2' . .	−12·5**	−9·7*	−11·8**	−6·0*
S.E. .	±2·99	±3·89	±3·36	±2·21

of K_m' show only a small and irregular variation, though relatively to the controls the increase is 12 per cent. for the best yielders and well over 100 per cent. for the worst. It has sometimes been suggested that economy might be effected by selecting only the good yielders for manuring, but this evidence is against such a practice so far as K is concerned, though it might be supported in the use of N. The differences between

TABLE 11. *Responses of Differing Classes of Palm, partitioning twenty-four inside palms by fives*

Cowan No. 2, 1942–54, kg./palm/annum.

Class	*Mean yield*	N_m'	P_m'	K_m'	*s.e.*	K_2'−K_1'	P_2'−P_1'
1	89·0	4·0	4·0	10·0*	±4·68	0·1	0·1
2	73·0	3·2	4·3	6·9	±3·77	1·0	−0·1
3	57·5	2·9	−0·1	11·7**	±2·99	4·7	−0·5
4	39·2	−1·4	−1·1	15·6**	±3·51	5·7	−1·0
5 (4 palms only)	15·6	−3·0	1·6	10·9*	±3·86	6·5	−0·6

K_2' and K_1' increase with regularity down the grading, suggesting that the requirement of K increases for the poorer palms. Because neighbouring palms compete by root-overlap the successful ones will tend to be found in the better grades and the losers (e.g. late supplies) in the lower grades. Hence the real amount of fertilizer acquired by the better classes of palms may be higher than that enjoyed by the poorer classes. These latter then appear in a lower position on the response-rate curve, which on the usual logarithmic law would show a greater difference between single and double rates. This argument supports liberal treatment of poorer palms with K as a relief to competition, and the table suggests

that the return would then be at the highest level in Class 4. The evidence regarding P responses is that, like those for N, the sign changes from positive for highly productive palms to negative for lower grades, and this comes entirely from growing detrimental effects of the double dressing of P down the grading. Such results have intensely practical implications and require more detailed and extensive examination, pending which further comment is reserved.

TABLE 12. *Mean Results of Leaf Analysis.*
Percentages in dry-matter

		K_2O	P_2O_5	CaO	MgO	*p.p.m.* Mn
J. B. Hale [2]. *1941. Selected palms.*						
Healthy	upper frond .	1·52	..	0·94	0·52	210
	middle ,, .	1·33	..	0·97	0·40	230
	lower ,, .	1·31	..	1·28	0·31	280
	Mean . .	1·39	..	1·06	0·41	240
Bronzed	upper frond .	1·65	..	0·84	0·52	150
	middle ,, .	0·67	..	1·43	0·54	250
	lower ,, .	0·66	..	1·56	0·55	370
	Mean . .	0·99	..	1·28	0·54	257

H. M. Gray. 1949. Selected palms.
(assuming 10% ash in dry matter)

						K_2O/P_2O_5 *ratio*
Control ($N_0P_0K_0$) .	0·99	0·50	1·58	0·47	..	1·97
Manured ($N_2P_2K_2$) .	1·69	0·60	1·52	0·31	..	2·83

Leaf analysis. Early in the experiments certain leaf analyses were made and reported by Hale [2] to investigate the possibility that a very prevalent bronzing of the palm leaves might be a symptom of K deficiency, and later, in 1949, Gray (private communication) carried out analyses on specimens from (000) and (222) plots at Cowan. A summary of the results is given in Table 12 for the completeness of this record. Hale's figures show the distribution of K to be more uniform in the healthy leaves, the bronzed leaves apparently exercising high translocation of K as they begin to fail. Even at an early stage of the high-manuring rate of the Cowan figures of Gray show a great increase in the K uptake, raising the K_2O/P_2O_5 ratio from 2 to 3. In their Malayan results Chapman and Gray [3] consider a ratio of 2 so low that a depression from P applications may be expected, and this seems to be supported by the results now described.

Effects on number of fruiting palms and of bunches produced. The data have so far been dealt with on the practical basis of weight of fruit per unit area (or planting point) and there has been found no reason to depart from this. It is of interest, however, to see what further information can be gleaned from bringing in the questions of numbers of bunches and

fruiting palms. This has been done in Table 13 using the last four years at Cowan, when the fertilizer effects on the whole physiology of the palms should be well established. The Mg treatment was given during this period and is seen to have been negligible in its effects. The figure for fruiting palms must be used with caution, for the non-fruiting members are excluded by years and a palm having no fruit in one year may reappear as a contributor in the next. K certainly increases the average number of palms fruiting in any year (i.e. it reduces the long pause-periods between fruitings), while N affects the figures as though it has a small opposite effect. P has produced its effects through number of bunches rather than by increasing their average weight, as indicated by the equivalence of the

TABLE 13. *Mean Effects compared on Fruit Weight and Bunch Number and corrected for non-fruiting palms (by years)*

Cowan 81 plots, 1951–4

		Mean	*Per cent. of relevant controls*				*Per cent. of mean s.e. per plot*
			N_m'	P_m'	K_m'	Mg_m'	
Per palm planted	Fruiting palms (by years)	84·5 per cent. of total	−1·6	0·5	7·6**	−1·0	6·38
	Bunches . .	4·14 per ann.	8·2**	5·0*	12·4**	0·7	7·64
	Fruit weight .	65·1 kg. per ann.	5·1*	5·6*	26·3**	0·0	8·70
Per fruiting palm	Bunches . .	4·89 per ann.	5·3**	4·7*	4·2*	1·5	7·41
	Fruit weight .	76·9 kg. per ann.	7·0**	5·4*	17·2**	0·7	7·94

response on the two measures of number and weight, while K has obviously increased the bunch number and then increased its influence further by increasing the average weight also. The increase in average bunch weight due to K was $1·8 \pm 0·23$ kg. on a control average of 14·0 kg. If a separation of function between the elements were marked its natural consequence would be the appearance of interactions, and these have not been general.

The data for bunch numbers at Ndian afford no special contrasts with the weight data already considered. The younger experiments, Nos. 1 and 3 Lisombe palm on sand, suggest a flush of bunch numbers caused by the first applications of N, but this did not persist and led to a negative N' on the regressions. Bunch numbers are higher in young palms. It is a general conclusion that bunch numbers would afford a most unsatisfactory criterion as a substitute for weights.

One clear but not very important association of average bunch weight is with the annual rain and yield cycle. On the monthly data covering nine years supplied by ninety-six Deli palms (two plots of No. 5 experiment Ndian) the average bunch weight was a minimum (17·8 kg.) at the middle of the dry season and also at the height of the rains. Presumably in the one case the lack of moisture is the cause, while in the other it is an effect of low insolation and exhaustion after high yields. Between these minima are two distinct maxima (20–21 kg.) about May and November corresponding to periods of moderate yield (52·5 kg./palm/annum) and sufficient rain and sun.

Residual effects. It will be evident from the continuous build-up shown by some effects of the treatments over many years, and from the fact that total application has been much in excess of removals by the crops, that there should be important residuals remaining in the site (in living palms, palm residues, and soil), having further potential values. The question naturally arises as to enhancing profits toward the end of the economic life of a stand by stopping expenditure on fertilizers some time in advance of felling. The case is presented in Fig. 2 for the large K effects on the Ndian gravelly clay comparing the mean effect of two levels with a histogram of costs. The last application there was for 1951 in anticipation that replanting would begin in 1954 or in 1955. The immediate reduction in effect suggests that any K retained on the site

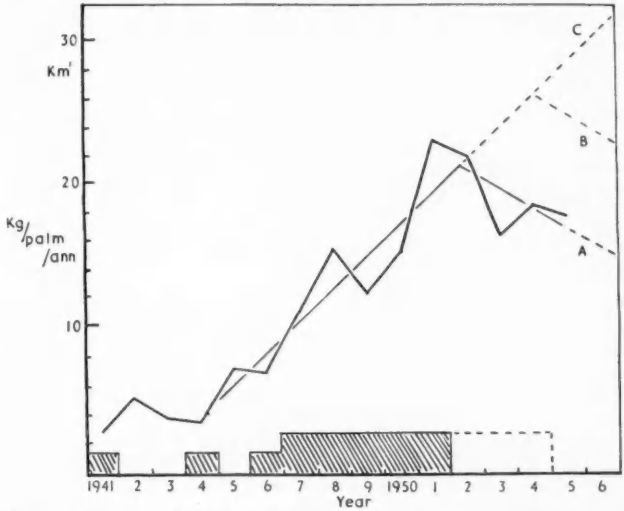


FIG. 2. Mean K effect on Ndian gravel, with histogram of costs, showing persistence after stopping treatment. Last treatment in 1951. A estimates yield effects to 1956. B and C estimate yield effects for continuance of treatment for three and for five years.

is not readily available. When the three-year rhythm is allowed for it is remarkable how closely the rise and fall of response is represented by straight lines of similar slope. The future course to the end of 1956 is predicted by the broken line A. Economic comparisons can be made from the appropriate areas in the diagram, and they indicate that during the five years of high manuring 1947–51 the profit was 3·9 times the cost, while during the next five years 1952–6, without further cost, the profits would mount by a further 5·4 times to a total of 9·3 times the outlay. If manuring had been continued an extrapolation of the linear regression, C, represents the probable course of events, while B is an intermediate forecast, had only three extra years of manuring been provided. The areas show that this latter course would have added to the gross profits though not to the rate of profit on expenditure, but it is to be noted that

this depends upon the very high returns in these two experiments. If the response should be lower, the value of the continuance of treatment diminishes until a point is reached where the advantage is on the side of the earlier stoppage.

Annual yield cycle. Oil palms show very marked fluctuations in yield, which must be understood for a proper appreciation and assessment of experimental results. The fundamental feature of the individual palm is an alternation between male and female flowering, which can be very irregular, but periods of four or five months each predominate. An inflorescence appears potentially in the axil of each frond. Eight consecutive fronds are required (circling the palm three times) to come back

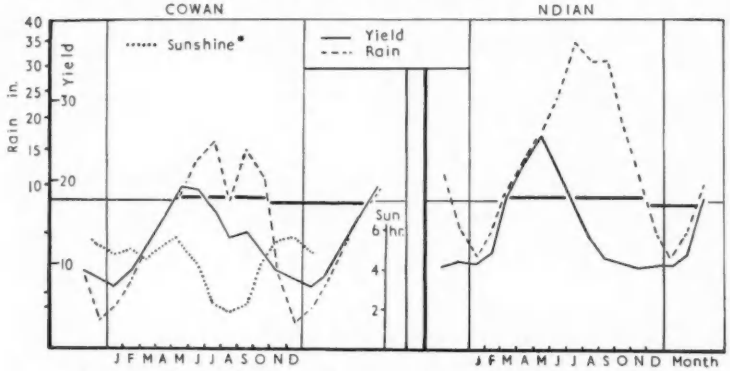


FIG. 3. Annual cycles of yield, sunshine, and rain, plotted by months. The line at 8·0 in. rain per month represents assumed sufficiency level.
* WAIFOR records, Benin.

to the same vertical line on the stem, which, with a rate of about twenty fronds per year, brings up the five-month period again as being that of a complete whorl. The pauses between fruiting periods have a modal value of five months but are often much longer, and the duration then shows peak frequencies at multiples of five months. Fruit ripens about six months after maturity of the female flowers.

The basic alternation in yield in Nigeria is an annual one imposed by the marked seasonal contrasts in sunshine and rainfall. Rainfall is adequate for the greater part of the year, but there is a dry season of some severity, while the sunshine becomes very deficient in the middle of the wet season. Fig. 3 compares the average annual cycles of rain and yield at the two estates, based on monthly averages (rain 1943–53, yields 1946–53 at Cowan, rain and yields 1940–9 at Ndian).

The sunshine curve at Benin (West African Institute for Oil-Palm Research) is also included. The rainfall has been plotted to a transformed scale using the square root of the rain when expressed in tenth-inches, so giving more weight to low rainfall than to high, which no doubt conforms better to the relative influences on the palms. To distinguish between periods of deficiency or excess a line has been drawn at the value corresponding to 8 in./month. This level of assumed sufficiency of rain

was arrived at from a general consideration of all the data, and, though higher estimates have been put forward, it is still high in the opinion of some experts. Ndian has much the higher rainfall, but at both estates the pattern is the same, with a very marked dry season around December or January and high rain from March to October or November. Fruiting activity of the palms (considered together) is continuous, but shows a rise in intensity of at least 100 per cent. concurrent with the onset of the rainy season. This activity lasts some three months, but then begins to decline before the rains reach their peak. The proportion of female flowers is low in July and high in October, influencing the yields in January and April in such a fashion as to synchronize with the rainfall changes and intensify the annual rhythm. The little peak of yield at Cowan in September may be attributed to a high female sex-ratio of flowers in March. An examination of an experiment at Cowan in a particular year revealed 54 per cent. of the palms fruiting during the half-year July to December, while in the first half of the year about 80 per cent. were fruitful and produced three times as much fruit per palm.

Although the behaviour described above is very distinctly and regularly followed over the areas and years indicated there can be very significant exceptions. The years 1950–3 at Ndian were not included in the averages because the seasonal effects on total estate yield had then quite disappeared. On examining the detailed behaviour of one half-plot of twenty-four Deli palms at Ndian (treatment $N_2P_1K_0$) it was found that, while an annual peak was always marked, it was in the normal position or early rainy season from 1941 to 1945, but then gradually shifted to later in the year, until in 1948 to 1952 it was quite late in the rainy season. This shift of six months or so would bring the annual rhythm into exact opposition to plots or fields following the normal rhythm. The same change was traced to an ageing effect in more complete data at Cowan and it is plain that it could contain the explanation of the more even spread of the Ndian estate yields which came about (through fields of varying ages).

Longer-term cycles of yield. Since the data have been recorded without break for so long they have served to reveal additional very distinct yield cycles with longer periods than one year. Most commonly a cycle of three or four years is followed by individual palms, the maxima being nearly four times the minima on the average. Palms with a common experience have some tendency to keep in phase so that rhythms remain when neighbours are combined into plots. A five-year rhythm appears when very large numbers of palms are combined or when the three-year cycle is suppressed by taking a running mean. The effect upon a conventional examination of yield figures will be obvious. Whenever an experimental grouping of palms is found to be giving a relatively high yield on the annual total, then, in as far as this means a predominance of palms at a peak in that year, there is present an expectation of a compensating downward movement one or two years later. In early years of experimental treatment, while effects are small, these natural movements may be several times as large as the treatment effects which are being sought, and apparent effects answering to significance tests may appear

in individual years which should not be ascribed to the relevant treatment itself, but to phase differences in rhythmic movements which form a sequence with events previous to the assignment of the plot treatments.

If we take as zero the time at which the primal flower bud developing in the heart of the palm is determined as female, then the emergence of its accompanying frond is at 14 months. Two or three months later the flower appears and passes through the greatest danger period for abortion at about 20 months.[1] At 24 months, if it survives, it is ready for pollination and a ripe fruit bunch is ready at 30 months. We only have to suppose a connexion between changing nutritional demands in the palm and the sex-ratio of primal flower-buds being formed at the same time (starvation tending to maleness) to have here a basis for a 5-year cycle. If an unusually high demand of ripening bunches were accompanied by a differentiation of a greater proportion of male primal buds then a reversed yield movement would occur 30 months later, which repeats as the inverse reaction to complete a cycle in 5 years. Such a reversal was noticed in a Malayan experiment[2] where an increase of yield procured by artificial pollination was followed by a depression due to a great increase in male flowers. The most frequent natural initiation of such a rhythm would follow from the first wave of production as palms mature, and such five-year waves are plainly to be observed in several cases which the authors have examined. In one case the first peak yield of an estate was followed by a gradual reaction to half this value, which in the absence of explanation caused some alarm, but recovery was complete by the fifth year on from that peak. In this case the best fit for the half-period of the cycle was 32 months, and the monthly deviations from the mean annual seasonal cycle had a regression coefficient on those of 32 months earlier of $-0{\cdot}520 \pm {\cdot}12$.

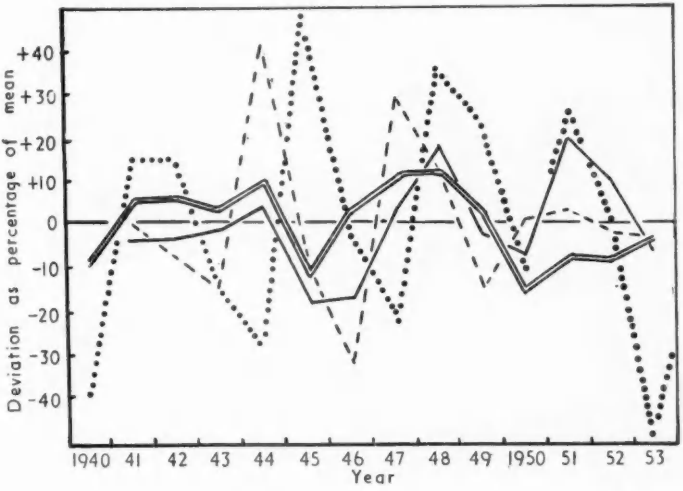
The common period which appears for individual palms or closely-bound groups is one of three years, which suggests some other mechanism overriding the one outlined above. On average a palm may produce four times as many fruit bunches in its peak years as in intervening bad years, with six fruiting months in the one case and only two in the other. The reason for the regularity of the recurrences might be sought in some reaction between season and the cycles of the palm itself, for if the latter integrate into a fundamental of 9 months this would produce a 'beat' of three-year periodicity (as in the theory of sound) when the pronounced seasonal cycle of 12 months is superimposed. The modal male-female cycle appears to be near the right length to suit this hypothesis but would require elaboration with considerations of further questions, such as sensitivity to abortion of flowers, before the wideness of the variations could be satisfactorily explained. If an explanation along these lines is finally established the phenomenon need not be expected to show in regions of more uniform seasons. At Kangala the three-year cycle is certainly not so apparent, although the five-year cycle is marked.

Devuyst [4] has used the basic periods of the palm with the object of

[1] We are indebted to Dr. A. F. M. Broekmans of the West African Institute for Oil Palm Research for permission to use here his results communicated to us and as yet unpublished.

[2] Private communication—Dr. G. W. Chapman.

forecasting yields from rain. He arrives at a figure for useful rain by discarding from monthly records all rain over 300 mm./month, and relates this to the bud formation which will eventuate as fruit some 33 months later. This relationship of yield to rain with the stated time-displacement is close in the data cited, but it is to be noted that the yields follow a very



••••• One palm.

– – – One plot of 24 palms.

——— All experiments, *c.* 3,000 palms.

═══ Whole estate *c.* 300,000 palms.

FIG. 4. Annual yield variation of palms at Ndian.

regular five-year cycle, and it seems unlikely that the yearly values are independent. In such case the determination of causality is not easy. These data from La Mé show rain to be in deficit for two seasons totalling nine or ten months of the year, while the data we are examining show rain mostly in excess. While Devuyst's useful rain ranges from 50 to 80 in./year, ours on the same basis would be 70–90 at Cowan and 105–120 at Ndian with only one short dry season. It is not surprising therefore that we have been unable to parallel his findings from a limited number of less variable seasons. But a three- to four-year cycle in yield is so general in the data of these experiments that the question of using it to assist in forecasting yields of sufficiently small units in similar localities could be approached with some confidence.

Examples of the periodicities are given in Figs. 4 and 5. Fig. 4 shows how they appear for differently-sized groups of palms on Ndian,

all plotted as annual values of the deviations (expressed as percentage) from the mean for the time covered. Individual palms of the half-plot studied show characteristic amplitudes, often very large. The example shown in dotted line in the diagram is the highest-yielding member of the

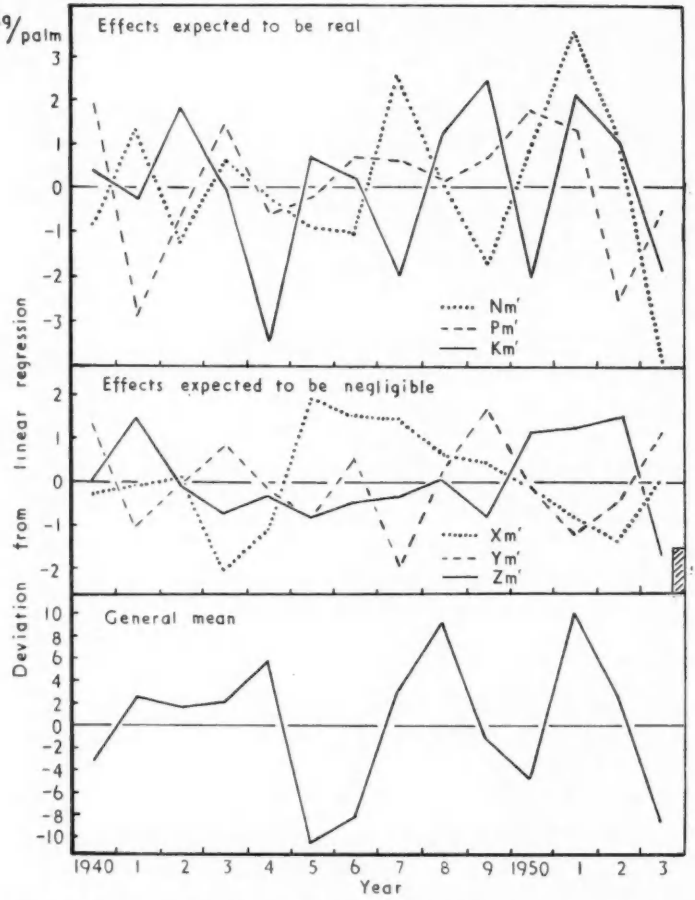


FIG. 5. Long-term cycles, averaging five Ndian experiments shown as annual deviations from the linear regressions. Real effects and high-order interactions compared with the general mean.

group, having an unusually small amplitude convenient for the scale. The three-year cycle is exact after the first—being out of step with the estate in 1945 and in step in 1950. The combination of all twenty-four palms in this particular plot is shown in broken line. The period is three years but not in step with the single member. The amplitude begins at

40 per cent. about the mean, but diminishes with time, and this damping is no doubt associated with slight progressive changes in the phase relationships of the individuals. Combining the palms to still larger numbers the yields of the inside palms for all experiments (135 plots × 24 palms) are plotted as a continuous line. The amplitude is reduced, but the rhythm remains, with a tendency to a lengthening of the period. The upward regression due to manuring may be noted. Finally, taking all palms of the estate, a rhythm with five-yearly minima remains (double line). The first minimum in 1945 is about five years from the beginning of general maturity, but the fields were of different ages and for nearly all of them it was a bad year. This suggests that some influence of weather, too remote to be definitely discernible in the records, impressed itself here, but a natural period in the palms probably helped the recurring minimum five years later. It is to be noted that the Kangala experiment, though so far distant but of similar age, also had yield minima in 1940, 1945, and 1950. It is obvious that there must be a strong tie of common experience binding the palms, but to separate the parts played by external season (the contrasts between years are not great) and by fundamental internal palm rhythms would require more extensive data than these.

In Fig. 5 the periodicities are illustrated as revealed by the differences in plot data by means of which manurial effects are measured. The complete data of the Ndian experiments have been used, namely 135 plots of 48 palms each. For each mean effect the calculation is made on the appropriate grouping, 45 plots appearing as control and 90 plots as receiving the treatment being measured. Linear regressions have been first taken out to provide a diagram of annual deviations therefrom. In the lower curve is given the periodicity of the plots as a whole to allow judgement as to the dependence of the other movements. It may be of significance that the time period shortens gradually from five years to three during the years represented. On the 'beat' hypothesis this would correspond to a decrease in the length of the supposed natural period of the palm from ten months to nine, attributable perhaps to ageing or to the gradual effects of manuring. The other two groups of curves show, first the fluctuations of the three main effects which in the design were expected to be real influences, and second, for comparison, three other items of variation calculated in the same way but representing high-order interactions between treatments, logically expected to be insignificant and conventionally assigned to error. It is seen that the harmonic movement of the real effects is much more definite and of greater amplitude than the three-factor interactions, although these latter still show a tendency to the three- or four-year periodicity. The treatments have always been applied in the dry season, so synchronizing with the annual rain influences, and it seems that they have impressed themselves to develop the natural rhythms, bringing them into greater regularity and prominence. K_m' follows a definite three-year cycle, with a significance better than $P = 0{\cdot}001$ on a harmonic analysis. N_m' follows a four-year cycle ($P = 0{\cdot}01$), with a marked building up of amplitude. P_m' also follows a four-year cycle, but this is less clear as the contributing

experiments are more diverse in their reactions to P. When it is considered that single experiments may have larger amplitudes than this average of five it will be seen how great a chance there is that one year's results, if read in isolation, could give a completely misleading measure of an effect, though answering well to tests of significance. The three elements seem to have similar degrees of influence on the rhythms though their ultimate effects on yields are quite dissimilar.

These illustrations have been introduced for cautionary more than for explanatory purposes, since the story has proved too kaleidoscopic for a clear and formal exposition. Small reliance can be placed on shorter periods than three years for experiments under these conditions. In particular the calculation of linear regressions from yield curves having such large and regular fluctuations, with wave lengths of several years, can be much influenced by the years chosen and must be approached with great caution, while if the phases are shifted by the treatments great confusion could ensue between what is permanent and what transitory.

Acknowledgements.—We wish to thank the United Africa Company Limited for permission to publish this paper. Thanks are also due especially to the estate staffs for the care and labour expended to produce such a long series of consistent records. Since each bunch of fruit produced was measured and recorded for the palm concerned the basic records had over three-quarters of a million effective entries.

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EXPERIMENTS ON TOBACCO-SEED PRODUCTION II. THE RELATIONSHIP BETWEEN RATE OF APPLIED NUTRIENTS, CHEMICAL COMPOSITION OF LEAF AND SEED YIELD

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Summary

Cured leaf of reaped and unreaped tobacco seed plants supplied with varying rates of nutrients was analysed for content of nitrogen, phosphorus, potassium, calcium, and magnesium. The results indicate that

(*a*) Reaping of leaf reduced the nutrient content of leaf from the top of the plant. This was associated with reduction in seed yield.

(*b*) Increasing the rate of application of phosphate from 100 to 200 lb. P_2O_5 per acre increased the content of this nutrient in the leaf. The best rate for seed production may be between these levels.

(*c*) Increasing the rate of application of potash from 100 to 200 lb. K_2O per acre increased the content of potassium in the earlier reapings. Luxury consumption may have been taking place at the higher rate.

(*d*) Application of magnesia had no significant effect on the content of any nutrient in the leaf.

A PREVIOUS paper [1] gave the results of experiments to determine the best method of tobacco-seed production. The present paper presents the results of chemical analysis of cured leaf from reaped and unreaped seed plants with nutrients applied at various levels, and discusses the relationship between these results and the previous findings.

Experimental Material and Methods

An experiment was conducted at the Kutsaga Tobacco Research Station in the 1953–4 season to investigate the effects of 'reaping' of leaf and of rates of application of nitrogen, phosphate, potash, and magnesia on yield and quality of tobacco seed produced. The design was a single replicate of a 3×2^4 factorial layout with certain three-factor interactions confounded to give four blocks of twelve plots each, with 14 degrees of freedom for error. The two-factor interaction Mg× Reaping was also partially confounded. The variety was Hicks.

Nitrogen, phosphate, potash, and magnesia were supplied as a mixture of sulphate of ammonia and nitrate of soda in equal parts, superphosphate, muriate and sulphate of potash (1 : 3 mixture), and magnesium sulphate.

Samples of cured leaf of good quality were retained from the first, third, and fifth reapings from the reaped plots. Leaf was sampled from the unreaped plots to correspond with the fifth reaping of the reaped plots and cured in the same barn. The first, third, and fifth reapings consisted of leaf from the bottom, middle, and top of the plant respectively. The first reaping was taken when most of the plants were coming into flower, the third when flowering was well advanced, and the fifth

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when flower heads were in full bloom and the first seed capsules were ripening. In the lamina of these leaf samples nitrogen, phosphorus, potassium, calcium, and magnesium were determined as follows:

Nitrogen. The Kjeldahl digestion technique was used. The ammonia was then determined by the diffusion method of Conway and Byrne [2] as modified by Hunter [3].

Phosphorus. The material was dry-ashed and the total phosphorus determined colorimetrically by Muir's modification [4] of the method of Shelton and Harper.

Potassium. Potassium was determined turbidimetrically in a HCl extract of the ash as described by Hunter [3].

Calcium. A turbidimetric method, outlined by Hunter and Hall [5], was used to determine the calcium in a HCl extract of the ash.

Magnesium. The absorptiometric method, based on the formation of a coloured complex of magnesium hydroxide with the dye Thiazol Yellow, of Hunter [6] was used; the determination was made on a HCl extract of the ash.

All results were expressed on a dry-matter basis, moisture content being determined by heating for 12 hours at 105° C.

Results

The design of the experiment did not allow full statistical analysis of data from reaped plots only. The confounding in the complete experiment produced a greater confounding in the reaped plots taken by themselves, and the main effect of magnesia and the phosphate × potash and nitrogen × magnesia interactions were mixed with block effects. Statistical analysis of the data from the reaped plots alone was therefore not undertaken and means only are quoted in Table 1.

The *nitrogen* content of the cured leaf decreased as reaping advanced, the main reduction being in the fifth reaping, in which the nitrogen content was only about half that of leaf reaped earlier. Raising the level of applied nitrogen from 24 to 57 to 90 lb. per acre was accompanied by an increase in the nitrogen content, the rise being greater from low to medium than from medium to high.

Mean *phosphorus* content was almost constant for all reapings and varied only slightly with different fertilizer applications. The higher rate of application of phosphate was consistently associated with a higher phosphorus content in the leaf.

The mean *potassium* content decreased with successive reapings. The higher level of potash application was associated with a large increase in potassium content in the early reapings, but none in the final reaping.

At the time of the first reaping, *magnesium* content varied to some extent with varying levels of application of nitrogen, phosphate, and potash but in the later reapings differences had almost vanished. Adding magnesia to the fertilizer was consistently associated with a rise in the leaf content of this nutrient. In all cases, the biggest fall in magnesium content occurred in the early stages of reaping.

Calcium content of leaf from the first reaping was considerably higher

TABLE I

Effect of Rate of Application of Nutrients on Leaf Content in Reaped Tobacco Plants

Treatment (*lb. per acre*)	*Nutrient content*														
	Nitrogen (N)			*Phosphorus* (P)			*Potassium* (K)			*Calcium* (Ca)			*Magnesium* (Mg)		
Reaping:	1	3	5	1	3	5	1	3	5	1	3	5	1	3	5
Nitrogen (N)															
24 . . .	4·5	4·2	2·0	0·28	0·30	0·34	2·0	1·6	1·6	3·0	2·0	2·0	0·66	0·47	0·34
57 . . .	5·2	5·0	2·6	0·28	0·31	0·29	3·7	2·2	1·5	3·3	2·2	2·1	1·09	0·46	0·35
90 . . .	5·8	5·3	2·7	0·34	0·32	0·27	3·1	2·8	1·2	3·2	2·2	2·0	1·00	0·46	0·37
Phosphate (P_2O_5)															
100 . . .	5·4	5·1	2·6	0·28	0·29	0·28	3·5	2·5	1·4	3·2	2·2	2·0	0·84	0·47	0·33
200 . . .	5·0	4·6	2·3	0·32	0·33	0·32	2·5	1·9	1·5	3·2	2·1	2·0	1·00	0·46	0·38
Potash (K_2O)															
100 . . .	5·1	4·7	2·4	0·30	0·33	0·32	2·6	1·5	1·4	3·2	2·2	2·0	0·83	0·43	0·36
200 . . .	5·2	5·0	2·5	0·30	0·30	0·28	3·3	2·8	1·4	3·1	2·1	2·0	1·02	0·50	0·34
Magnesia (MgO)															
0 . . .	5·0	4·9	2·4	0·30	0·31	0·30	3·3	1·8	1·4	3·1	2·2	2·0	0·71	0·43	0·31
30 . . .	5·3	4·8	2·5	0·31	0·31	0·30	2·7	2·5	1·5	3·3	2·1	2·0	1·14	0·50	0·40
General mean .	5·2	4·8	2·4	0·30	0·31	0·30	3·0	2·2	1·4	3·2	2·1	2·0	0·92	0·46	0·35

than in the two later reapings. Varying rates of application of nutrients gave no appreciable or consistent differences in calcium content.

Top leaf from all plots. As all plots were represented, it was possible here to make the full analysis of variance. Results are presented in Table 2. Seed yields are also included for convenience.

TABLE 2

Effect of Leaf Reaping and Rate of Application of Nutrient on Content of Top Leaf and on Seed Yield

Treatment (*lb. per acre*)	*Nitrogen* (N%)	*Phosphorus* (P%)	*Potassium* (K%)	*Calcium* (Ca%)	*Magnesium* (Mg%)	*Seed yield* (*lb./acre*)
Leaf reaping:						
Not reaped	2·9	0·35	3·0	2·2	0·40	374
Reaped	2·4	0·30	1·4	2·0	0·35	319
Nitrogen, (N)						
24	2·2	0·35	2·4	2·0	0·35	258
57	2·8	0·32	2·3	2·1	0·38	377
90	2·9	0·30	2·0	2·2	0·39	404
Phosphate (P_2O_5)						
100	2·7	0·31	2·3	2·1	0·37	350
200	2·6	0·34	2·2	2·1	0·37	342
Potash (K_2O)						
100	2·7	0·33	2·2	2·1	0·38	346
200	2·7	0·31	2·3	2·1	0·36	347
Magnesia (MgO)						
0	2·6	0·33	2·2	2·1	0·35	357
30	2·7	0·32	2·2	2·1	0·40	335
S.E. ± 2-factor	0·09	0·01	0·09	0·03	0·04	14
S.E. ± 3-factor	0·11	0·01	0·11	0·03	0·04	17

Note. All values rounded to two significant figures.

When leaf was reaped, the nutrient content of top leaf was reduced. The largest effect was on potassium which was significantly lowered by over half. Nitrogen, phosphorus, and calcium contents were also significantly reduced but the difference in magnesium content was not significant.

Increasing the rate of application of nitrogen from 24 to 57 lb. per acre gave a significant increase in content of nitrogen in top leaf; with 90 lb. per acre there was a further non-significant increase. Increasing the rate of application of phosphate increased the phosphorus content of the top leaf; no effect on the content of other nutrients was found. Varying magnesia or potash applications had no significant effect on nutrient content.

Discussion

Reaping of leaf. As stated in a previous paper [1] this practice resulted in reduced seed yields and may be considered detrimental. The explanation may be found in the nutrient content of leaf.

Previous workers have reported the translocation of nutrients from the

vegetative to the reproductive plant organs during flowering. Morgan and Street [7] stated that nitrogen uptake from the soil was rapidly approaching cessation eighty days after transplanting and that building up of nitrogen in the seed capsules of the untopped plant occurred largely at the expense of its leaves. Loew [8] noted the tendency of magnesium and phosphorus to accumulate in the seed, and Garner [9] described movement of essential nutrients from older to younger leaves and finally to the flower and seed structures.

In the author's experiments chemical analysis of leaf from the bottom and middle of the plant showed that at the onset of flowering, such leaf contained large quantities of nutrients which would be lost to the plant in normal reaping. In unreaped plants, as the lower leaf approached senescence the nutrients apparently tended to move into the younger tissues and into the developing seed. This is suggested by the nutrient content of top leaf which was in all cases less in reaped than in unreaped plants. The effect on potassium content was particularly large.

Rate of application of nutrients. Nitrogen. The previous paper [1] reported the beneficial effect of heavy nitrogen dressings, the rate recommended for the type of soil on which the experiments were carried out being 60 lb. N per acre. This rate agrees well with the nitrogen content of top leaf, which was significantly increased with rates up to 57 lb. per acre, the further increase over this rate being non-significant. The importance of nitrogen in tobacco-seed production has been pointed out by Garner [9] and by Vickery *et al.* [10], and the increase in nitrogen uptake emphasizes the benefit of the heavier dressings.

Phosphate. No response in seed yield was obtained by increasing phosphate application over 100 lb. P_2O_5 per acre. Nutrient content of leaf was unaffected except for phosphorus itself, which was significantly increased. Komatsu [11] observed that up to 130 lb. of P_2O_5 per acre increased yield of dry matter and rate of phosphorus absorption by the plant but with larger dressings yield and absorption decreased. This may be why the higher rate of application proved ineffectual. In the author's experiments the concentration of phosphorus in bottom, middle, and top leaves was about equal. For tomatoes, according to Eckerson [12], this implies that the plant is receiving too little phosphorus. In his investigations, plants receiving sufficient phosphorus showed a steady increase from the bottom of the plant to the young growth at the top. It is thus possible that the best rate of application of phosphate lies between 100 and 200 lb. P_2O_5 per acre.

Potash. The gradient of potash concentration from high at the bottom of the plant to low at the top is stated by Gribbins *et al.* [13] to indicate a high level of supply. This effect was obtained in the author's experiments with the lower as well as the higher rate of application and may explain why, as previously stated [1], seed yield showed no improvement with the higher rate, when luxury consumption may have been taking place.

Magnesia. No significant effect resulted from the application of magnesia. Magnesium content of the leaf was never less than 0·31 per cent. Mg, concentrations in lower leaves being much higher than those in

upper leaves. This is said by Garner *et al.* [14] to show an ample uptake by the plant, and the addition of magnesia to the fertilizer is therefore not necessary in normal circumstances.

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PRIMARY AND SECONDARY SEX RATIOS IN DOMESTIC FOWL

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(*Ministry of Agriculture, Fisheries, and Food*)

Summary

An account is given of the conflicting views on the secondary sex ratio in fowl. Attention is drawn to the general assumption that the primary sex ratio is one of equality. From the data obtained from a number of hatcheries where manual sexing is practised a slight excess of males over females appears to be common although, because of the limitations of manual sexing, this might equally be taken for a slight excess of females. The records of the hatcheries investigated show a slight excess of females in the summer although this appears to be more than offset by the slightly greater excess of males in the spring and winter. Inquiry showed that although hatchings from all eggs set were lower in the summer this was entirely due to lowered fertility at that time.

On the basis of this material and the results of experimental work with a flock of White Leghorns in which details of embryonic deaths, sex at hatching, and mortality over 8 weeks were recorded the following conclusions are drawn:

1. The primary sex ratio shows an excess of females. This excess may possibly be smaller with crossbreeds than with purebreeds.
2. Embryonic female mortality usually exceeds that for males. This difference is normally increased when hatching levels are poor.
3. Poor hatching rates thus result in an increase in the proportion of males at the secondary stage; the ratio may rise to above 50 per cent. males. Good hatching, on the other hand, results in a greater proportion of females at the secondary stage.
4. There is a seasonal variation in the secondary sex ratio. It is tentatively suggested that this is possibly due to the effect of age or protracted laying, resulting in a greater excess of females at fertilization than that found with young parents.
5. Differences between mortality rates for males and females in the pre-natal period do not persist in the rearing stage after hatching. It is not permissible, therefore, to conclude that with fowl the female, being the heterogametic sex, suffers in a precisely analogous way to the male with mammals. Nor has any evidence been found to indicate that heterosis resulting from cross-breeding influences the viability of the female either pre-natally or after hatching.
6. The only hypothesis which can be offered at present to explain the higher embryonic mortality of female fowl is that there are sex-linked genes which influence only pre-natal not post-natal viability.

OPINIONS on the secondary sex ratio (i.e. at hatching) of domestic fowl differ. Some workers maintain that more female chicks are normally hatched; others incline to the contrary view. Most of these workers have stated or implied that the primary sex ratio (i.e. at fertilization) is 50:50. None appears to have opposed the conclusions to be drawn from the early work of Pearl [1]. Although he appears to believe that there may be equality of sexes at fertilization, he found 48·58 per cent. males at hatching with families of ten chicks or more, and argued 'that pre-natal mortality is not differential in respect to sex and that in consequence the observed sex ratio at birth is substantially the same as the initial

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zygotic sex ratio'. In view of Pearl's own findings that the percentage of males at hatching was below 50 per cent., this must be taken to imply the view that fewer male embryos are formed at fertilization.

The literature on the secondary sex ratio is extensive but, as already stated, the conclusions are in conflict. Hays [2] has stated that the primary sex ratio is about 50:50 although considerable differences may exist between families. Hays [3] has also stated that the embryonic death-rate of females is greater than that of males at all stages of development. On this basis it could be assumed that more males would be hatched, and Hays did find this to be so to a slight extent [4]. Mussehl [5] presented evidence that the sex ratio of 1,514 chicks hatched from a flock under his management was 52·24 per cent. males. In opposition to this view are the conclusions of Landauer and Landauer [6] who refer to a sex ratio of 48·57 per cent. males in 5,421 hatched Leghorn chicks. They drew attention to the figures for 67,993 chicks from numerous observations by other workers which when combined give a sex ratio of 48·77 per cent. males at hatching. Landauer and Landauer also refer to the mortality rate of 52·7 per cent. males in their chicks (excluding death by accident) from day-old until 8 weeks. On the basis of this evidence they suggest that more males than females die during early post-natal life and conclude from this and from the sex ratio at hatching that, similarly, a higher male mortality occurs in the pre-natal stage, i.e. more males die during embryonic development. Their arguments are based on the assumption that there is equality of sexes at fertilization.

This opinion of Landauer and Landauer is not conceded by Byerly and Jull [7]. Among 17,989 chick embryos examined by them which had died after the ninth day of incubation they found 47·56 per cent. males. The possibility that more male than female embryos died before the ninth day of incubation is considered by them but, on the basis of work carried out by one of them [8], it is concluded from indirect evidence that there is no difference between the sexes in mortality rates during the early period of incubation. (Hays [3], however, submits evidence pointing to a higher female embryonic-mortality rate during the first 5 days of incubation.) No evidence was found by Byerly and Jull to indicate that post-natal mortality rates differed between the sexes. They found a sex ratio at hatching of 50·1 per cent. males and, among a larger number of chicks recorded, the survivors to 10 weeks of age showed a ratio of slightly over 50 per cent. males. They conclude that, if differential embryonic mortality exists, the female sex suffers more than the male, and they tentatively ascribe this condition to sex-linked genes which impair viability.

Two hypotheses have been advanced by the supporters of the two schools of thought which hold either that more males or more females survive after fertilization. Hays points out that in fowl the female is the heterogametic sex and, therefore, a higher female embryonic mortality rate would be analagous to the higher male pre-natal and early post-natal mortality generally observed with mammals (including the human species), where the male is the heterogametic sex. Landauer and Landauer argue that on this basis more female than male chick embryos

should die and, after hatching, this differential should be continued during the early post-hatching period. As they found more females at the secondary stage (hatching) and more males dying during the early post-natal period, they dissent from the view postulated by Hays—with the assumption that the sex ratio at fertilization is 50:50. They also point out that no generally accepted explanation exists for the greater male mortality among human infants. They suggest that the higher male mammal mortality, and their opinion that a similar state of affairs holds good for the male sex with fowl, can be attributed to the higher basal metabolism of the male.

Experimental

In an attempt to resolve these conflicting views sexing records for one year from a number of reputable hatcheries were collected; and further, the sex ratios for hatched chicks and dead embryos in a flock of White Leghorns managed under the author's supervision were recorded over two years.

The total number of chicks sexed manually by the participating hatcheries in 1954 was 13,910,703. The proportion of males was 50·088 per cent.; the hatching rate of fertile eggs (assumed infertiles judged by candling only) was 82·3 per cent. This result would suggest an almost equal secondary sex ratio and possibly a slight excess of males. Unfortunately manual sexing is not fully accurate; males recorded as females may amount to some 3 or 4 per cent. A similar chance of error in the reverse direction might be assumed, but as female chicks form the most important part of the hatcheries' trade it is customary to classify as males any chicks over which the sexer is doubtful. If an allowance for this bias is made, the real proportion of males in the chicks examined would be slightly below ·50 per cent. At one hatchery, however, sex-linked chicks were produced, and of the 41,768 chicks sexed by down colour 51·9 per cent. were males—a figure significantly greater than 50 per cent. It is of interest to record that the hatching rate with these cross-bred birds was only 59 per cent. and evidence will be presented later to support the hypothesis that the secondary sex ratio is influenced by the hatching rate.

The data collected from the participating hatcheries related to hatchings carried out throughout 12 months. In the reports of the several workers cited above little information is given about the time when the hatchings took place and rarely is the rate of hatching given. The sex ratios recorded for successive monthly hatches at one hatchery were examined for 1952–5 and in each year the same broad pattern was evident. This showed a decline in the number of males during June to September (Fig. 1). The average for each year—except 1952—showed (on the basis of manual sexing) a slight excess of males (Table 1); the spring and winter showed an excess of males more than sufficient to offset the slight excess of females recorded in each summer and autumn.

Since the hatchery figures related almost entirely to crossbreeds and so-called hybrids, the sex ratios of a flock of White Leghorns managed by the author were also recorded for 1954 and 1955. This flock was

established in 1946 and has been closed since that year. The stock was purchased from seventeen widely separated breeders and no doubt the matings in the early years resulted in a good deal of heterosis. In recent years some measure of inbreeding has resulted from the closing of the

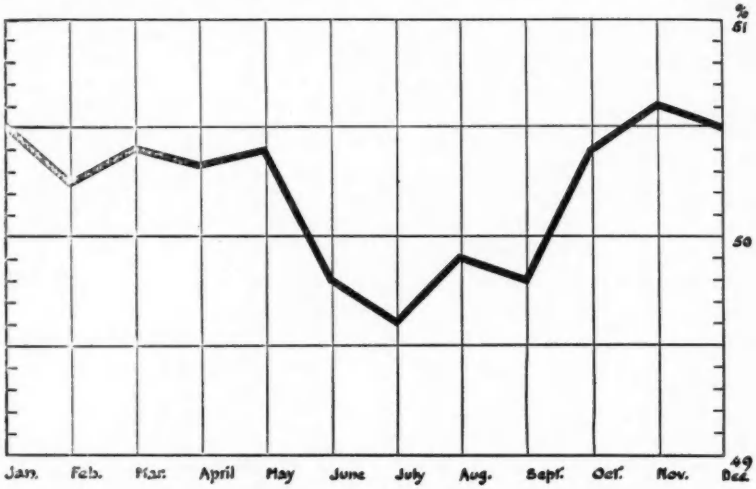

FIG 1. Percentage of males hatched each month. Average monthly figures over 4 years relating to 6 million chicks (approx.) from one hatchery.

flock, although hatching rates have been moderately good (about 80 per cent. of fertile eggs) in the last five years. Manual sexing is not carried out but sexes are determined by inspection at 6 to 8 weeks; all birds dying or culled are sexed in a post-mortem examination. All eggs pro-

TABLE 1. *Sexing Results at One Hatchery 1952–5 (Manual Sexing)*

Year	*Chicks hatched*	*% Males*
1952	909,242	49·7
1953	1,551,018	50·5
1954	1,392,085	50·4
1955 (ending Sept.)	1,330,775	50·6

duced (other than those cracked or very badly misshapen) are set, the first hatch being taken off each year in early March and the last towards the close of May. All eggs failing to produce a chick are opened and, if fertile, the stage when the embryo died is recorded. If death is found to have occurred after the tenth day of incubation the sex is determined.

The results for the pullets mated in 1954 and 1955 are set out in Table 2. From these results the secondary sex ratio in the 5,146 chicks hatched was found to be 48·95 per cent. males. The hatching rates for the two years differed materially. This appeared to be due to an experimental diet in 1955 which led to a decline in the hatching rate from

79 per cent. in 1954 to 61·9 in 1955. The cause of this decline seemed to be the adverse influence on the chick embryos, on the nineteenth day of incubation, of something in the fish meal in the diet [9]. Had the previous year's mortality rate operated at the nineteenth day of incubation the hatching rate would have exceeded 80 per cent. In both years a

TABLE 2. *Sex at Hatching and Sex of Embryos Dying after 10 Days of Incubation, in a Flock of White Leghorns, 1954 and 1955*

	1954	1955
Fertile eggs	2,798	4,598
Dead in shell	588 (21%)	1,662 (36%)
Chicks hatched	2,210	2,936
Male	1,076	1,443
Female	1,134	1,493
Dead embryos		
Male	175	476
Female	245	852
Unidentified (i.e. before 10 days)	168	332

high proportion of embryonic deaths occurred after the tenth day of incubation, when the sex was fairly easily distinguishable. In 1954 the percentage of embryonic deaths after the tenth day was 71·4; and in 1955, 77.

TABLE 3. *Record of Embryonic Deaths, and Chicks Hatched, in a Flock of White Leghorns, 1954 and 1955*

	1954		1955	
	Males	*Females*	*Males*	*Females*
Sex of hatched chicks	1,076	1,134	1,443	1,493
Sexed embryos	175	245	476	852
Unsexed embryos (assume 50:50)	84	84	166	166
Total	1,335	1,463	2,085	2,511
Primary sex ratio	47·7%* males ± 0·9%		45·4%† males ± 0·7%	
Secondary sex ratio	48·7% males ± 1·1%		49·1% males ± 0·9%	
Mean P.S.R.	46·25%† males ± 0·6%			
Mean S.S.R.	48·95% males ± 0·7%			

* = Significant at P = 0·05. † = Significant at P = 0·01.

In both years the embryonic death-rate after the tenth day of incubation showed an excess of females. In the second year (1955), in which the hatching rate was substantially lower, the female embryonic death-rate was much greater than in 1954 with its normal hatching level. If the early embryonic deaths in which sex could not be determined are assumed to have had an equal sex ratio, the primary sex ratios for 1954 and 1955 were 47·7 and 45·37 per cent. males. The secondary sex ratios for the two years were 48·7 and 49·1 per cent. males respectively. The primary sex ratios are significantly less than 50 per cent.; the secondary ratios are not. For the combined figures for the two years the primary and secondary sex ratios are 46·25 and 48·95 per cent. males respectively (Table 3). It is of interest to observe that in 1955 had the entire group

of unidentified early dead embryos been classed as males, the total would still indicate an excess of females at the primary stage.

Discussion

The primary sex ratio for the White Leghorns showed a percentage of males significantly less than 50 in both years. The secondary sex ratio was also less than 50 per cent. males in both years but not statistically significantly so. In this respect the results do not materially differ from those recorded by Byerly and Jull, who found a secondary sex ratio of 50·1 per cent. males, nor are they in opposition to the results from the massed figures from the hatcheries investigated, assuming that those figures, resulting from manual sexing, correctly represent the true ratio. But they are not in agreement with the secondary sex ratio statistically

TABLE 4. *Secondary Sex Ratios and Hatching Rates for Sex-linked Crosses at one Hatchery (1952–5)*

Year	*Nos. of chicks hatched*	*Hatching rates (%) of fertile eggs*	*Males (%)*
1952	2,991	92·3	49·9
1953	7,105	78·8	50·6
1954	13,588	54·5	51·3
1955	11,569	86·4	50·0

significantly less than 50 per cent. males, as reported by Landauer and Landauer and many other workers. Neither do they accord with the result recorded for the sex-linked chicks, which showed a sex ratio of significantly more than 50 per cent. males—but with a low rate of hatching.

These divergences may be resolved by a consideration of hatching rates, breeds or crossbreeds involved, and the period during the year when hatching took place.

In the White Leghorn flock under discussion it was noticed that the secondary sex ratio showed a slight but statistically insignificant increase in males associated with a substantial decline in hatching rates. It is commonly reported by hatcheries that during the main hatching period, i.e. January to May, declines in hatching rates are usually accompanied by an increase in the percentage of male chicks. This would suggest that in the normal hatching season high hatching rates result in a fall in the proportion of males at hatching below 50 per cent., while with moderate hatching levels this proportion approaches parity and with poor hatching results it may exceed 50 per cent. This explanation may account for the excess of males with the sex-linked chicks, for which a sex ratio of 51·9 per cent. males was recorded but where the hatching rate of fertile eggs was only 59 per cent.

This opinion gains further weight from the data supplied by one hatchery for its sex-linked crosses over four years. It will be seen from Table 4 that the percentage of males at hatching was substantially above 50 per cent. as hatching rates declined in 1953 and 1954; a reverse trend was apparent when hatching improved in 1955.

Moderate hatching rates may also afford reasons for the hatcheries investigated showing a slight excess of males. Although an average hatching rate of 82·3 per cent. of fertile eggs is claimed for these hatcheries it is doubtful whether this figure can be substantiated. The average figure for most hatcheries barely exceeds 70 per cent. of all eggs set [10]. It is known that fair numbers of eggs classed by the hatchery owner as 'clear' or infertile are in fact fertile eggs in which the embryo has died at an early stage. At some hatcheries also, eggs with early dead germs, when detected, are removed from the incubator and disregarded when calculating the hatchability rate. Unfortunately Byerly and Jull do not give the average hatching rate for the stock on which their conclusions on secondary sex ratios are based. It is clear, however, that many were crossbreeds, and the nature of the parent stock, whether pure or cross-mated, seems to be of some importance.

Most workers apparently agree (with the exception of Landauer and Landauer), and it is confirmed by this experiment with White Leghorns, that more females than males die during embryonic development, particularly if incubation conditions are adverse. If the sexes were equal at the primary stage an excess of males at the secondary stage would be a logical expectation. In this experiment with Leghorns and in many of the experiments cited this expectation was not fulfilled. The explanation would seem to be that the primary sex ratio is not equal, i.e. more females than males are produced at fertilization; this hypothesis will be argued later. Assuming that the evidence justifies this view for White Leghorns, does it apply equally to other pure breeds and cross-breeds? The point is of interest because some of the earlier work appears to have been carried out with pure breeds, while crossbreeds figure largely in later experiments. In recent years there has been a material increase in the proportionate numbers of crossbreds distributed by hatcheries; more recently still, increased numbers of so-called hybrids have been supplied.

Huxley [11] has postulated that with the human species, where the male is the heterogametic sex, adverse conditions intensify and favourable ones neutralize differential male mortality during pregnancy. Lenz [12] and Huxley have also advanced the hypothesis that with mammals recessive sex-linked factors, with a slightly deleterious effect upon viability, account for the greater mortality among human males. Huxley further postulated that male children of wide racial crosses showed a greater survival before and after birth and this he ascribed to heterosis 'enabling the male to resist the deleterious effect of harmful sex limited factors'.

If Huxley's first two above-mentioned postulates applied in reverse to fowl, in which the female is the heterogametic sex, they would require more females to die during embryonic development, and, under relatively adverse hatching conditions, proportionately more males to survive at the hatching stage. This appears to be so in the experiment here described. But on the same argument more females should die in the initial rearing stages, which does not seem to apply in the post-natal life with fowl. It might be further argued, if Huxley's further postulate

last-mentioned above is similarly applied in reverse to fowl, that with crossbreeds and hybrids more females should appear at the secondary stage than with pure-bred stock.

These general conclusions would be based on the assumption of an equal primary sex ratio; this, it has been argued, does not always appear to apply with fowl. In the present experiment with pure-bred White Leghorns the first postulate seems to be satisfied, and it does seem widely accepted that more females than males die before hatching. But apart from the evidence offered by Landauer and Landauer there seems to be little data to support the contention that a greater proportion of either sex die in the early rearing stage. Byerly and Jull did not find a post-natal differential mortality. In this experiment with White Leghorns there was no significant difference between the mortality of the two sexes at 8 weeks (Table 5). In spite of the fact that the chicks

TABLE 5. *Hatching Rates and Post-hatching Mortality in a Flock of White Leghorns, 1954 and 1955*

	1954	*1955*
Hatching rate	79%	64%
Number of chicks hatched	2,210	2,938
Sex ratio at hatching	48·7% males	49·1% males
Mortality to 6 weeks from hatching	4·1%	16·5%
Sex ratio at 6 weeks	48·7% males	49·0% males

in 1955 were apparently subject to greater stress owing to the experimental diet and had a mortality rate at 6 weeks of over 16 per cent., the sex ratio at 8 weeks showed no appreciable change from the secondary sex ratio. The second above-mentioned postulate of Huxley does not therefore seem to apply in relation to fowl. The application of Huxley's first-mentioned postulate, however, seems to be valid since, with poor hatching owing to poor incubation or non-genetical causes operating during incubation, the proportion of males at hatching increases and may exceed 50 per cent.

This point seems related to the possible influence of heterosis with crossbreeds in increasing the survival chances of the heterogametic sex, i.e. the female with fowl. On the evidence of the hatcheries there seem to be no grounds for believing that crossbreeding results in any improvement in the survival rate of the female. Indeed, as the numbers of crossbreeds at hatcheries have increased there is a tendency for the secondary sex ratio to evince an increased percentage of males over females (Table 1). From the evidence supplied by records of sex-linked stock two sets of conditions appear in conflict. A low level of hatching would lead to the expectation of an above-average number of males because of heavy female pre-natal mortality; if Huxley's argument be accepted the heterosis effect, with an equal primary sex ratio, should result in more females surviving than males. If these two expected tendencies do in fact both operate the secondary sex ratio would embody the result of their joint effect—i.e. they would tend to cancel out or show ratios which might vary considerably with different crosses and different

hatching rates. Another explanation might be that with crossbreeds the primary sex ratio more nearly approaches 50:50 and in consequence the normal higher embryonic female mortality would lead to a secondary sex ratio in which males exceeded females, i.e. the heterosis or other effect of the wide cross would be confined to influencing the primary sex ratio. This excess of males would be more marked with poorer hatching. This second explanation, viz. that crossbreeds compared with pure breeds have a primary sex ratio nearer 50:50, but that deleterious sex-linked genes affect the viability of females pre-natally, appears to fit the conditions with fowl better than the theory that heterosis induced by crossbreeding would improve viability among female embryos. The known facts would not support the latter nor would the apparent absence of differential mortality *after* hatching (which absence is widely reported and also found in this experiment) support a theory that the rate of survival of females is influenced by heterosis, for neither with pure-breeds nor crossbreeds is there any evidence—apart from that offered by Landauer and Landauer—that post-natal mortality varies, no matter to what extent differential mortality prevailed prior to hatching.

It seems to be generally assumed by all workers, with the possible exception of Pearl, that the primary sex ratio is 50:50. The evidence afforded by this experiment with White Leghorns indicates that equality in the primary sex ratio is not realized. Even if one makes the unlikely assumption that all or most of the embryos dying in the first 10 days of incubation are males the results for 1955 still show an excess of females. It may also be that the primary sex ratio differs with different breeds and strains. It seems, however, unlikely that this is so, apart from a slightly closer approach to, but not actually achievement of, equality with crossbreeds. If the primary sex ratio were in fact 50:50 one would expect commercial hatcheries to obtain a secondary hatching rate with males showing well above 50 per cent., for it is clear that the average hatching rate of commercial hatcheries is not high and it seems generally agreed that under adverse or even moderately good incubation conditions more embryo females die. It seems, however, relatively rare for the numbers of males to exceed 51 per cent. at the secondary stage. With dead in shell averaging about 20 per cent. of all fertile eggs set, and accompanied by a substantial excess of dead female embryos over males, it seems most unlikely that under these conditions the primary sex ratio can be 50:50. It is therefore concluded that during the normal breeding period the primary sex ratio manifests an excess of females; this excess may be diminished when crossbreeding is in force, but not to the point where parity is realized.

There seems some reason to believe that these conclusions may not hold good throughout the year or during periods other than the normal hatching season, i.e. November to May. Reference has already been made to the marked seasonal change in the secondary sex ratio recorded each year at one hatchery (Fig. 1). This pattern was repeated each year with very slight variations and is commonly reported by hatcheries. Although hatches of all eggs set during the summer are usually poor, detailed examination of the hatching rates did not reveal, over the

months, any material variation in the hatching rate of fertile eggs, the poor hatches in the summer being solely due to a decrease in the percentage of fertile eggs. It will, however, be realized that hatchings from June until October relate to eggs produced from breeding stock at the end of their first laying year; the hatchings from October onwards normally relate to the new season's pullets hatched earlier in the same year. If with these summer hatchings embryonic mortality of females still exceeds that for males, it would seem reasonable to conclude that with age—or long-continued laying—the primary sex ratio widens and substantially more females than males are produced at fertilization.

In the experiment with White Leghorns described a number of second-year birds were recorded in 1955 and, although few in number (16), the results give some colour to the hypothesis. The results are set

TABLE 6. *Embryonic Mortality and Sex Ratio Recorded for Sixteen Second-year Dams*

	Males	*Females*
Embryonic deaths after 10 days' incubation	66	113
Sexes at hatching	133	135
Total	199	248
Primary sex ratio	44·5 per cent. males	

out in Table 6 and it will be apparent that the primary sex ratio in the progeny of these hens manifested a higher percentage of females than that found with the progeny of the pullets. In spite, too, of a much heavier female than male embryonic mortality the secondary sex ratio showed a very slight excess of females. These figures are far too small for significance but, allied with the commonly repeated seasonal pattern reported by hatcheries, they are compatible with the suggestion that age or protracted egg production may influence the primary sex ratio. It should be pointed out that this finding is not in accordance with the views of Hays and Spear [13] who contended that older parents produced more male chicks surviving at 8 weeks of age, and it has been argued by several workers that differential mortality between the sexes does not occur prior to this age. Nevertheless the excess of females regularly reported by hatcheries at the end of the season cannot be disregarded.

The main conclusions arising from the above discussion are embodied in the Summary at the beginning of this paper.

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THE GENE Sr Ka 1 IN RELATION TO THE RESISTANCE OF WHEAT TO *PUCCINIA GRAMINIS TRITICI*

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Summary

Evidence is presented which indicates that a number of wheat varieties possess a common gene Sr Ka 1 for resistance to *Puccinia graminis tritici*. It would appear that this gene is effective against a number of physiologic races including race 15B. It is apparently ineffective against race 49. Available evidence suggests that the protective action of this gene tends to disappear when plants are kept at constant high temperatures.

Three varieties were shown to possess a different inherent resistance which is reflected in a differential behaviour to various physiologic races.

A plea is made for the establishment of an internationally recognized centre vested with the responsibility of maintaining authentic 'type' material.

In recent years it has become apparent that effective breeding programmes for the control of wheat stem rust must in future be based on the use of a diversified range of 'resistant' genes. Elsewhere [1, 2] the author has outlined the principles involved and has stressed the need for more extensive genetic studies of the available parental material. At the present time long lists of resistant varieties are nothing more than an embarrassment to wheat breeders, faced as they are with the task of choosing parents for their crossing programmes.

The studies reported herein were initiated at the Waite Agricultural Research Institute, South Australia, in 1952 and continued at Wagga, New South Wales, during 1954 and 1955. The experimental work consisted of a genetic analysis of a number of wheat varieties using Australian races of *Puccinia graminis tritici*.

From the somewhat parallel behaviour which has been reported for many of the selected varieties, it was felt that perhaps such varieties might possess a common basis for resistance and experiments were designed to test this hypothesis. Other varieties were selected because they were known to behave differentially to rust races occurring overseas.

As the work proceeded it became clear that, with respect to Australian races, the behaviour of many of the varieties was governed by a single gene common to those varieties. This gene was designated Sr Ka 1 by Athwal and Watson [3] who accepted the system of nomenclature proposed by Ausemus *et al.* [4]. Watson and Waterhouse [5] identified this gene in several varieties, three of which—Eureka, Kenya S.U.743, and Kenya 122.D.I.T.(L)—were included in the present study.

Following upon the genetic studies a survey of the literature was made with a view to ascertaining what might be expected when the gene Sr Ka 1 is exposed to other races of *P. graminis tritici*. Certain tentative conclusions were reached in this survey, and although their confirmation must necessarily await further genetic studies with those races, the

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TABLE 1. *Origin and Identification of Wheat Varieties used in Genetic Analysis*

Group	Variety	Seed source	United States Dept. Agric. C.I. No.	United States Dept. Agric. P.I. No.	N.S.W. Dept. Agric. Accession No.	Sydney University Accession No. (S.U.)	Canada R.L. No.	Remarks
A	Eureka . . .	1952 World Wheat entry 8	..	134044	C. 12503	1311	1534	Derived from Kenya N.B.F6.K.2.G6A.9(L)
„	Kenya N.B.F6.K2.G6. A.9(L)	„ 21	..	124736	C. 6040	743	1513	Also designated P.I.103539
„	Kenya R.F.324 .	„ 24	12882	118896	C. 9906	1456	1387	Also designated P.I.117768
„	Kenya N.B.263J(L) .	„ 25	..	117526	C. 9968	1458	1356	California No. 3098
„	Kenya 117.1.5.F(L) .	„ 26	..	124742	C. 10861	1482	1377	Also designated S.U.1465 and R.L.1–40–40
„	Kenya 130.B.6.B .	„ 28	..	117775	C. 10866	1472	1358	Also designated S.U.1473 and P.I.118904
„	Kenya 117A . .	„ 30	12568	..	..	..	1–49–64	Distinct from Sydney Univ. and Kenya strain
„	Kenya 122.D.I.T.(L) .	„ 31	12186	..	..	1478	1373	Also designated S.U.1304
„	Kenya 291.J.1.I.1. .	„ 35	..	177172	..	1350	1–48–41	Derived from Kenya 58.F(L)1
„	McMurachy . .	„ 51	11876	..	C. 12451	1488	1313	Selection made at Manitoba 1930
„	No. 43 . . .	„ 66	..	159106	..	..	..	..
„	Onas 52 . . .	„ 279	..	..	..	..	..	Derived from KenyaN.B.263.J(L)
„	Negroz 11–45 .	Brazil ..	..	..	..	..	..	..
„	Kenya 58.F(L)1 .	Kenya ..	..	..	..	1487	1–34–4	Also designated E144 in India
„	Kenya 112A . .	„ ..	..	..	..	..	1–35–4	..
B	Kenya B.286 . .	1952 World Wheat entry 22	..	124738	C. 6042	745	1–40–34	Also designated P.I.103540
„	Kenya 338.AC.2.E.2 .	„ 33	12880	187165	..	..	1–49–89	Recently named 'Kenya Farmer'
„	Kenya 321.B.T.1.B.1 .	„ 37	..	177179	..	..	..	..

information presented in this paper should serve as a useful guide in the planning of breeding programmes.

Materials and Methods

Most of the varieties included in this investigation have been the subject of study by other workers [5, 6, 7, 8, 9, 10]. The varieties together with their respective identification numbers are listed in Table 1. Fifteen were obtained from the United States Department of Agriculture, having been included in their 1952 list of World Wheats. Two were obtained through the courtesy of H. C. Thorpe of Kenya and one from the Instituto Agronomico do Sul, Brazil. It should be emphasized that Kenya 117A (World Wheat 30) is quite distinct from a variety of the same name which has been the subject of studies by Athwal and Watson [3] and obtained by them from Kenya.

Two races of *P. graminis tritici* were used, designated 126 and 222AB by Waterhouse [11] and lately referred to by Watson [12] as 126 Anz 1 and 222 Anz 2 respectively. All varieties were resistant to race 126 Anz 1 and all with the exception of Kenya B.286 were resistant to race 222 Anz 2. The Australian variety Federation was used as a common susceptible parent in the genetic studies with race 222 Anz 2.

All pathogenicity tests were conducted in an unheated greenhouse during the winter months. In all cases the infection ratings were made on seedlings in the two-leaf stage.

Results of Genetic Studies

Altogether thirty-eight crosses were made for pathogenetic studies in the F.2 generation.

The results of F.2 segregations for crosses between Federation and each of nine resistant varieties of group A are set out in Table 2. In all

TABLE 2. *Reactions of F2 of Crosses between Federation and Resistant Varieties of Group A when Inoculated with Race 222 Anz 2* P. graminis tritici

Cross	*Resistant*	*Susceptible*	*P value* (3:1)
Federation × Kenya R.F.324	40	10	> 0·3
,, × Kenya N.B.263J(L)	23	6	> 0·5
,, × Kenya 117A	35	13	> 0·7
,, × Kenya 112.D.I.T.(L)	28	8	> 0·5
,, × Kenya 291.J.1.I.1	28	13	> 0·3
,, × No. 43	36	13	> 0·5
,, × Onas 52	35	10	> 0·5
,, × Negroz 11–45	48	12	> 0·3
,, × Kenya 58.F(L)1	38	10	> 0·5

cases a single gene difference with dominance of resistance was indicated. Crosses between the remaining six varieties of group A and Federation were not available. However, Kenya 112A was crossed with Insignia 49, which is susceptible to race 222 Anz 2, and the F.2 segregated sixty-two resistant and nineteen susceptible (P value, 3:1, > 0·7).

Single gene differences for Eureka and Kenya N.B.F6.K.2.G6.A.9 (L) were reported by Watson and Waterhouse [5].

The results of intercrossing resistant varieties of Group A are set out in Table 3. Although all possible paired crossings were not made, each variety was crossed with at least one other member of this group. In all cases the F.2 populations failed to segregate for susceptibility. The sizes of the populations were such as to detect a different independently inherited gene at P = 0·95 level of probability. The absence of susceptible segregates indicates that the fifteen varieties of group A most probably share a common gene for resistance. However, the possibility that different linked genes may be involved should not be overlooked although the evidence presented in the next section adds confirmation to the former view that the fifteen varieties do in fact share a common gene for resistance to race 222 Anz 2.

TABLE 3. *Reactions of F2 of Crosses between Resistant Varieties of Group A when Inoculated with Race 222 Anz 2* P. graminis tritici

Cross	*Resistant*	*Susceptible*	*Cross*	*Resistant*	*Susceptible*
Eureka × Kenya R.F.324	74	0	Kenya 117A × Negroz 11–45	71	0
,, × Kenya 130.B.6.B	77	0	,, × Kenya N.B.263J(L)	47	0
,, × Kenya 117A	63	0	,, × Kenya 58.F(L)1	57	0
,, × No. 43	69	0	Kenya 58.F(L)1 × Kenya 112A.	59	0
,, × Onas 52	60	0	,, × McMurachy.	49	0
,, × Negroz 11–45	68	0	,, × Kenya N.B.F6.K2. G6.A.9(L)	60	0
,, × Kenya 112A	54	0	Kenya N.B.F6.K.2G6.A.9(L) × Kenya 130.B.6.B.	50	0
,, × Kenya 291.J.1.I.1	70	0	Kenya N.B.F6.K.2.G6.A.9.(L) × Kenya 117.1.5.F(L).	50	0
Kenya 291.J.1.I.1. × Kenya 117A	50	0			
Kenya 291.J.1.I.1. × Kenya R.F.324	77	0			
Kenya 117A × No. 43	61	0			
,, × Onas 52	53	0			

The three varieties of group B have been so grouped because all evidence indicates that each possesses a resistance distinct from that possessed by the varieties of group A.

Kenya B.286 has been shown [3] to possess the gene Sr Kc 1 which confers resistance against race 126 Anz 1 but which is ineffective against race 222 Anz 2. Dihybrid segregation of susceptibility was observed in an F.2 of Kenya B.286 × Onas 52 using race 126 Anz 1 to which both parents were resistant. Using race 222 Anz 2 the F.2 of Kenya 338.A.C.2.E (resistant) × Kenya B.286 (susceptible) segregated in a monohybrid manner.

The resistance of Kenya 338.A.C.2.E to race 222 Anz 2 appeared to be governed by a single incompletely dominant gene when this variety was crossed with the susceptible Federation. Susceptible segregates were secured when F.2 populations of Kenya 338.A.C.2.E × Eureka and Kenya 338.A.C.2.E × Kenya 117A were inoculated with race 222 Anz 2.

Likewise the resistance of Kenya 321.B.T.1.B.1 to race 222 Anz 2 appeared to be governed by a single incompletely dominant gene when crossed with Federation. Susceptible segregates were obtained when this variety was crossed with each of the three varieties of group A—Eureka, Kenya 117A, and No. 43 using race 222 Anz 2 as the inoculum.

At the same time it is not possible to differentiate completely between the genes for resistance of Kenya 338.A.C.2.E. and Kenya 321.B.T.1.B.1, since the cross between these varieties was not available for testing. However, the resistant reactions differ from each other, suggesting a different basis for resistance in these varieties.

Reactions of Varieties to Other Races of P. graminis tritici

It is of considerable interest to determine how far the conclusions drawn from the genetic studies conform with the observations recorded by workers using other races of *P. graminis tritici*. For example, the question might be asked: do varieties of group A behave in a parallel manner to other races? Similarly, do varieties of group B differ in their reactions to such races? In general, the extensive literature on wheat stem rust supports the results of the present genetic studies.

Newton, Johnson, and Peturson [13] tested four group-A varieties—Eureka, Kenya 122.D.I.T.(L), Kenya 117.1.5.F.(L), and McMurachy—to the twenty races 9, 10, 11, 15, 17, 19, 21, 29, 32, 34, 36, 38, 39, 48, 50, 56, 113, 120, 139, and 152 and found each immune in the seedling stage at ordinary temperatures (55 to 80° F. daily). The immunity tended to disappear when the plants were kept at a constant high temperature (75 to 80° F.).

Goulden and Stevenson *et al.* [14] state that two group-A varieties—McMurachy and Kenya 122.D.I.T.(L)—together with the variety Red Egyptian possess a common gene conferring resistance to race 15B. This gene controlled all races of stem rust tested up to that time in the rust area of western Canada under field conditions.

Genetic studies on the resistance of Kenya wheats to the Australian race 126 Anz 1 carried out by Waterhouse and Watson [5] indicated that three group-A varieties—Eureka, Kenya N.B.F6.K.2.G6.A.9.(L), and Kenya 122.D.I.T.(L)—contain the same gene for resistance to this Australian race of stem rust.

Lowther [6], recording the seedling reactions of nine group-A varieties to races 11, 15B, 17, 19, 36, 38, 56, and 59, found them all resistant at low temperatures (65–70°) and, with two exceptions, susceptible at higher temperatures (80–85°). The three group-B varieties were also examined but in no case was a decrease in resistance at higher temperatures observed.

Loegering [7] recorded the seedling reactions of seven group-A varieties and the three group-B varieties to the races used by Lowther [6]. His results confirmed those of Lowther except for some differences with race 59. Loegering also included results with races 32, 49, and 139 and found varieties of group A uniformly resistant to race 32 and generally susceptible to races 49 and 139 except for the moderate resistance of variety No. 43. Varieties of group B were again quite distinct in their reactions to races 49 and 139, each being resistant.

A uniform susceptibility of twelve group-A varieties to race 49 in Mexico was also reported by Bayles, Borlaug, and Kingslover [8].

Athwal [9] reports a uniform resistance of eight group-A varieties to races 14, 15c, 21, 34, and 40.

Three group-A varieties are of particular interest in that comparative tests with Kenya stem-rust races (10) clearly demonstrate differential reactions of these varieties when inoculated with eight Kenya races of *P. graminis tritici*. The reactions of the three varieties to the Kenya races are set out in Table 4.

Clearly the data of Table 4 suggest that the varieties Kenya 291.J.1.I.1, Kenya 58.F(L)1, and Kenya 112.A differ in genetic constitution with respect to stem-rust resistance. Assuming the identity of the three varieties to be correct, the Kenya data would suggest that

TABLE 4. *Reactions of Three Varieties to Eight Races of* P. graminis tritici

Variety	*Race*							
	K1	K2	K3	K4	K5	K6	K7	K8
Kenya 291.J.1.I.1. .	R	R	R	R	R	R	R	R
Kenya 58.F(L)1 . .	R	R	R	R	S	R	R	R
Kenya 112.A . .	R	S	R	R	S	R	S	S

R = resistant S = susceptible

other genes are operative in this material. Such a situation can be anticipated when a breeding programme such as the Kenya one embraces a variety of sources of resistance. Furthermore, the work of Athwal and Watson [3] has demonstrated the presence of several genes in Kenya material.

Conclusions

Although so much remains to be learned regarding the genetic control of stem rust, the evidence from the genetic analysis presented in this paper, linked with the independent varietal studies made by various workers throughout the world, helps considerably in systematizing existing knowledge. Such knowledge should lead to the planning of more effective breeding programmes in the future.

It would appear that the gene Sr Ka 1 is widely distributed in parental varieties currently used by wheat breeders. Confirmatory evidence regarding the identity of the gene in such varieties might well be secured through the use of aneuploid analysis, a technique evolved by E. R. Sears in the United States. Peterson and Campbell [15] have used this method in locating on chromosome XX a gene for stem-rust resistance in the variety McMurachy.

The gene Sr Ka 1 is certainly effective in controlling races 126 Anz 1 and 222 Anz 2 in Australia and it would appear to be effective against a number of races in other countries including 15B in North America.

The ineffectiveness of Sr Ka 1 against Australian race 126 Anz 2 is generally recognized and a similar ineffectiveness against race 49 in North America has been reported by a number of workers. The situation with respect to race 139 needs further investigation, for although Loegering [7] reported group-A varieties as susceptible to this race, Newton, Johnson, and Peturson [13] found three group-A varieties resistant.

In correlating the studies of various workers caution must be exercised regarding the actual identity of both varietal material and the physiologic races used. Much confusion has already been encountered with Kenya 117A where at least two distinct wheats have been listed under this single name. The need for the establishment of an internationally recognized centre vested with the responsibility of maintaining authentic 'type' material of known genetic constitution is essential if work of the type referred to above is to be extended.

Not only may different varieties be listed under a common name, but a single variety not infrequently receives a varied number of designations. For example, Kenya 58.F(L)1 is referred to in India as E144, so that it may be that the reactions of E144 listed by Gokhale [16] could well be equated with those of the group-A varieties carrying the gene Sr Ka 1.

Since completing the present study field observations suggest that two group-A varieties Kenya R.F.324 and Kenya 117A are identical and also with Kenya 58 listed in the 1952 World Wheat catalogue as entry 29. Situations such as these cause much needless confusion in breeding programmes and add further weight to the need for an internationally recognized 'type' collection of varieties.

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SOME OBSERVATIONS ON NATURAL AND ESTABLISHED PASTURES AND PASTURE PLANTS IN THE SUDAN RAINLANDS

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Summary

Observations on rain-grown pastures and pasture plants, both natural and sown or introduced, at Tozi Research Farm in the clay plains of the central Sudan are recorded. The soils are alkaline (pH 8·5–9·0 and over) and crack deeply in the seven dry months of the year. The rainfall is around 28 in. per year, falling from June to October.

The natural pasturage is of upright annual grasses, one of the most important being *anis*, *Sorghum purpureo-sericeum*. The grazing can be severely damaged, because of its habit, if taken at all intensively in the growing season. It is normally used only by the herds of nomads who move north and east out of the wetter rainlands during the wet season, to escape Tabanid flies, and under this seasonal utilization the grazing is apparently permanent.

For more intensive utilization a local strain of Rhodes grass (*Chloris gayana*) appears to be more suitable than any of the introduced species tested. It is perennial and palatable, can readily be established from seed, grows rapidly, and spreads by means of runners, particularly when grazed. It is tolerant of flooding. Although an excessively long or hot dry season may reduce the survival of plants, Rhodes grass should re-establish itself from self-set seed. Another useful grass, producing a great bulk of foliage, is the very palatable annual *Brachiaria obtusiflora* which is particularly at home in flooded areas and is also readily established from seed.

A number of species of herbaceous or lightly woody legumes are wild in the area and many of them have been sown and maintained in observation plots, as possible components of grass-legume mixed pastures. The most promising are *Clitoria ternatea*, *Glycine borianii*, and *Indigofera subulata*, which are either truly perennial or else readily self-sown.

A mixed stand of Rhodes grass and *Clitoria ternatea* has been established from seed on 55 acres at Tozi in a low-lying area subject to rain flooding. The seasonal use of such permanent pastures together with feeding of residues of sorghum and groundnut crops would provide a useful means of associating some stock with arable development in the region. Useful silage has been made from a mixed sowing of green gram and sorghum.

THE observations recorded in this paper were made in the East Central Sudan at the Central Rainlands Research Station, Tozi (N. lat. 12°, 30′; E. long. 34°), 10 miles west of the Blue Nile and 100 miles south of Sennar at a little below 1,500 ft. elevation. This station was opened in 1952 to provide data for the development of agricultural production on the clay plains of the Sudan in the 25- to 35-in. rainfall belt. Work on grasses and pasture plants is subsidiary to the main programmes on crops such as cotton, sorghum, groundnuts, sesame, and maize.

The expected average annual rainfall at Tozi is 28 in. Most of the rain falls between mid-June and early October; practically none falls in the remaining months of the year. During July, August, and September, the wettest months, maximum and minimum air temperatures remain

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steady around 30 and 20° C. respectively, and the dew point during this time is constant at about 20° C. The end of the rainy season in late October is marked by an abrupt drop in dew point from 20 to below 10° C., when the North African intertropical front, moving southward, passes Tozi. The diurnal range of temperatures then increases and, though the nights in December and January may be cool, the maximum temperatures rise markedly to reach a mean monthly dry-season level of 35 to 40° C., with temperatures of up to 43° C. recorded on some days. The dry season is long as well as hot, lasting from late October to the end of May.

The soils are deep alluvial alkaline clays having a pH of 8·5 to 9, and a montmorillonitic-clay content of 69 per cent. The topography is very flat. On slightly more elevated sites the soils are dark or very dark grey-brown (10 YR 3-4/2)[1], while the lower-lying soils, often flooded in the rainy season, are grey-brown (2·5 Y 5/2) or grey (10 YR 5/1). As it dries after the rains, the soil breaks into hard prismatic blocks separated by cracks up to 4 feet deep and 2 to 6 inches wide at the surface, narrowing downwards. The seasonal cracking, which breaks many of the finer plant roots, and the long-continued high temperatures of the dry season particularly near the dark-coloured soil surface, lessen the chances of survival of perennial herbs from one season to the next. The herbaceous flora at Tozi is composed mainly of annuals.

The vegetation, an *Acacia seyal–A. fistula* woodland associated with *Acacia campylacantha*, *A. drepanolobium*, and *Balanites aegyptiaca*, and containing areas of open grassland, closely resembles similar communities growing on the valley floor *mbugas* of central Tanganyika except for the absence at Tozi of certain perennial grasses, notably *Themeda triandra*.

Through much of the rainy period, from mid-July to September, the activities of biting Tabanid flies, collectively known in Sudan Arabic as *serut*, compel the nomadic cattle owners of the area to migrate northwards ahead of the fly to drier regions, or to the narrow belt of better drained *kerrib* soils of the erosion slope bordering the Blue Nile. The herds move south again with the onset of the dry season. During the Tabanid invasion the Tozi dairy herd is brought indoors from about 10 a.m. to 4 p.m. when the flies are most troublesome. Their grazing is thus restricted to about 6 hours each day. The Tabanids and the distance from markets are among the factors at present restricting the development of a cattle or dairy industry in the area, for which the vigorous growth of grass and the availability of crop residues may in time lead it to be seriously considered. It was as a contribution to this prospect that the present work was undertaken. The results have some relevance to the search for legume-grass pasture mixtures for the tropics.

Natural Pastures

The dominant wild grasses, many of which grow to a height of 6–10 ft., are short-lived; they set seed and dry out completely as soon as the rains are over. The main species, in the more open woodland or on treeless *sagiyas* (open grassland), are *Sorghum purpureo-sericeum*, *Hypar-*

[1] Munsell colour notation.

rhenia sp., *Rottboellia exaltata*, *Sorghum* spp. (*adar*), *Cymbopogon nervatus*, *Brachiaria obtusiflora*, and, in the denser woodland, *Beckeropsis nubica*. Of these species, only *Brachiaria obtusiflora* extends to the low-lying wet grey clays, where it generally occurs in pure communities but may sometimes be mixed with *Eriochloa nubica*. The main annuals will not stand heavy grazing: they can readily be prevented from seeding, and so eliminated, by relatively light grazing in the rains. The seasonal utilization imposed by the Tabanids, the annual firing of the bush as the nomads return, and the severity of the dry season are the main factors perpetuating the annual character of the pastures. Certain perennial species are found. Some, such as *Chloris gayana* (Rhodes grass) and *Cynodon dactylon*, occur in very small and localized communities, while others, such as *Setaria incrassata* and *Ischaemum brachyatherum*, are more widespread, though the total area they cover is minute in comparison with the annual species.

The characteristic grasses of disturbed sites are *Pennisetum schweinfurthii*, on old areas of cultivation; *Pennisetum ramosum*, common on margins of villages; and the short tufted grasses, *Chloris virgata*, *Digitaria gazensis*, *Dactyloctenium aegypticum*, *Dinebra retroflexa*, *Eleusine indica*, *Eragrostis* spp., and *Sporobolus cordofanus*, which replace the taller-growing species on areas of continued disturbance.

The grassland is remarkably rich in legumes. Altogether about seventeen species of legumes occur in it, although apparently some of them, such as *Crotalaria* sp. *aff. C. astragalina* and *Cassia* spp. are not readily taken by stock, especially when other grazing is available. The commonest species are the perennials, *Clitoria ternatea*, *Glycine borianii*, *Rhynchosia minima* var. *prostrata*, *Vigna vexillata*, and the annuals, *Desmodium dichotomum* and *Vigna pubigera*. In addition to grasses and legumes, livestock frequently feed on many other wild herbs, of which the most important is probably the perennial *Ipomoea cordofana*. Camels and goats take the flowers, pods, and leaves of acacia trees and shrubs. At Tozi the natural feed of the dairy herd is supplemented with groundnut hay and sorghum grain and stubble.

Legume and Grass Observation Plots

A number of grasses and herbaceous legumes have been grown in observation plots at Tozi, and are listed on p. 188. Some of these are wild Sudan plants, seed of which was first collected at Tozi in 1952, while others were introduced from Tanganyika, Southern Rhodesia, and Kenya.

Grasses

Chloris gayana. Of the five varieties of Rhodes grass tested, the Tozi strain is the most promising as it survives the dry season better than the introduced types. It is also probably better adapted to the markedly alkaline soil condition. The original plot of this variety, sown in 1953, has persisted strongly for three seasons. A larger plot (0·75 acres) of this strain sown on 20 July 1954 grew vigorously and was first grazed on 18 September. In 1955 the plot came away well at the start of the rainy season and was grazed regularly from July onwards. Later in the season it showed symptoms of nitrogen deficiency. Half of the plot was treated

Grasses	*Received from*
Brachiaria brizantha	Tanganyika
Brachiaria obtusiflora	Sudan
Bothriochloa insculpta	Kenya
Chloris gayana	Sudan
C. gayana	Tanganyika
C. gayana (Nzoia)	Kenya
C. gayana (Giant Rhodes)	S. Rhodesia
C. gayana (Katambora)	S. Rhodesia
Cenchrus ciliaris	Tanganyika
C. ciliaris (Chipinga)	S. Rhodesia
Cynodon dactylon	Sudan
C. plectostachyum	Tanganyika
Panicum coloratum var. *makarikari* (Bambatsi strain)	S. Rhodesia
Setaria incrassata	Sudan
S. sphacelata	Tanganyika
Legumes	
Clitoria ternatea	Kenya
C. ternatea	Australia ex Wad Medani
C. ternatea	Sudan
Crotalaria sp. *aff. astragalina*	Sudan
Dolichos daltoni	Sudan
Glycine borianii	Sudan
Indigofera hochstetteri	Sudan
I. parviflora	Sudan
I. subulata	Sudan
I. tettensis	Kenya
Phaseolus mungo	Sudan
Tephrosia uniflora	Sudan
Vigna pubigera	Sudan
V. vexillata	Sudan

with ammonium phosphate at 2 cwt./acre in late August. There was a very marked and rapid response, and by mid-September the herbage was dark green in colour. It is possible, therefore, that on the heavy clays at Tozi, on which responses to nitrogen (but not generally to other nutrients) are common though usually not large, nitrogen fertilizer might be useful in certain seasons to maintain the vigour of perennial grass pastures.

Brachiaria obtusiflora. A leafy, annual grass growing to a height of from 6 to 10 ft. It is considered to be the most palatable annual grass in the Sudan and has been grown with success under irrigation in the Gezira cotton area [1]. At Tozi it has grown well on an observation plot for 3 years; in the latter two seasons this was from self-sown seed. It tolerates long periods of flooding and is thus a useful grass to plant on low-lying wet areas, though it does equally well on better-drained soils. Being an upright annual, it would, however, be sensitive to grazing during the growing period.

Cynodon spp. The perennial *Cynodon dactylon* (Tozi strain), which survives the dry season, grew well in both 1954 and 1955 from stolons transplanted on 10 July 1954, though in both years lateral growth was rather slow at the beginning of the season. It has a soft, palatable foliage which is often taken in preference to other grasses, either annual or perennial. *Cynodon plectostachyum* (from East Africa) made poor growth when first planted in 1953 and did not shoot again in 1954.

Setaria spp. *Setaria incrassata*, a local tufted perennial, grows vigorously and generally survives the dry season. It is not, however, of much value for livestock as it flowers early and the herbage soon becomes tough and coarse. *Setaria sphacelata* made fair growth when first planted in 1953 but failed to grow again in 1954.

Panicum coloratum var. *makarikari* (Bambatsi strain). Although, apart from the difference in altitude and dry-season temperatures, the natural habitat of this strain, the Bambatsi Pan on the Nata River in Southern Rhodesia [2], is somewhat similar to the clay plains of the Sudan, this grass has never done as well at Tozi as in Southern Rhodesia where it is a promising pasture grass [2]. The vegetative growth at Tozi was fair but it was not as vigorous as the local *Chloris gayana*. It did not always survive the dry season well: only 40 per cent. of the plants on a plot first sown in 1953 grew again in 1954. In another plot, sown in 1954, most of the plants grew again in 1955.

Cenchrus ciliaris. Both the Chipinga (S. Rhodesia) and Tanganyika strains have done well on small observation plots for 3 years. Dry-season survival has been fairly good, but these grasses have not been tested on a field scale.

Other species. *Bothriochloa insculpta*, which grew well when first planted in 1953, did not set seed or grow again in 1954. *Brachiaria brizantha* made moderate growth in 1953, but no plants survived the dry season.

Legumes

Clitoria spp. Three strains of *Clitoria ternatea*, originally sown on observation plots in 1953, survived the dry season and came into leaf after the first showers in 1954. They produced a mass of vegetative growth in July and August. The semi-upright Australian variety (ex Wad Medani) was affected early in the season by a virus-like leaf disease, which ultimately destroyed the herbage, but the Kenya variety, which was only slightly affected, and the truly prostrate Tozi strain, which appears resistant to the disease, grew well throughout the rains. In the next season, the third from planting, the Tozi form soon produced a good cover, but only a few plants (less than 5 per cent.) of the other two strains grew again. Two larger observation plots of the Tozi (0·1 acres) and Wad Medani (1·0 acre) strains, planted on 18 July 1954, were grazed late in that season and throughout the 1955 rainy season, from July onwards. The Medani strain was again affected by the virus-like disease in the second year of growth, but not so seriously as on the smaller observation plot in the previous year.

Tephrosia uniflora. This is an upright, somewhat woody herb growing

to a height of from 1 to 3 ft. Although only about 50 to 60 per cent. of the plants survived the dry season, self-sown plants soon appeared at the start of the rains and, together with the perennating plants, produced a good cover. The species has not yet been tested on a field scale, but other species in this genus are known to be toxic [3].

Indigofera spp. *Indigofera subulata* and *Indigofera tettensis* are the most promising of the four species tested at Tozi. The other two, *Indigofera hochstetteri* and *I. parviflora*, died out after the first season and there was no regrowth from self-sown seed. *Indigofera subulata*, an erect herb, from 1 to 3 ft. high, with about the same nutritive value as the temperate legumes, vetch, and sainfoin [4], persisted for two seasons only, although there was fair regrowth from self-sown seed in the third year. About half the plants in an observation plot of *Indigofera tettensis* grew again in the third year, but in this case regrowth from self-sown seed was negligible.

Dolichos daltoni. This species, a semi-prostrate twining annual, does not produce as much herbage as the other legumes described here, but it persists each year from self-sown seed, and might do well in mixed legume and grass pastures.

Glycine borianii. This prostrate twining plant has persisted well as a perennial and from self-sown seed for three seasons on an observation plot. As with *Dolichos daltoni*, it might do well in mixed grass and legume pastures.

Vigna spp. The annual *Vigna pubigera* and the perennial *Vigna vexillata* (*babun*), both semi-prostrate twining plants with hairy stems and leaves, have grown well on observation plots for 3 years. *Vigna pubigera* came away well each season from self-sown seed, while *Vigna vexillata* is a true perennial. Neither is particularly palatable and they are not taken by stock if alternative grazing is available.

Phaseolus mungo. A twining perennial. It produced less herbage than *Vigna* spp. and was not readily eaten by livestock.

Other wild legumes. Six other legumes, namely *Alysicarpus glumaceus*, *Cassia tora*, *C. mimosoides*, *Tephrosia kotschyana*, *Desmodium dichotomum*, and *Rhynchosia minima* var. *prostrata*, grow wild at Tozi but all of them are inferior as forage crops to Clitoria and some of the other species described above. The Cassia species, *Rhynchosia minima* var. *prostrata* and *Tephrosia kotschyana*, are very unpalatable, while *Alysicarpus glumaceus* is an erect stemmy plant producing but little foliage. *Desmodium dichotomum* does not appear to be taken well by stock at Tozi though many other species of this genus are grown successfully as forage crops in other parts of the world [3].

Annual forage legumes. Several species of annual forage legumes do well at Tozi, especially cowpea, velvet bean, and green gram, each of which can be interplanted with sorghum for silage. In 1954 a silage mixture of Wad Akr sorghum and green gram, sown in alternate rows on 24 July, was ensiled on 11–12 October. The silage produced appeared of good quality and was readily taken by stock. In the same season, cowpea, variety Brabham, made better vegetative growth than green gram, and seems to be the better of the two for a mixed sorghum and

legume silage crop. It is likely, too, that good silage could be made from wild annual grasses.

Mixed Grass-and-Legume Pastures

Mixed grass-and-legume pastures were tested for the first time at Tozi in 1955. An area of about 55 acres, excised from the cultivated land because parts of it are liable to flooding during the rains, was sown, with a seed drill, with *Clitoria ternatea* (Wad Medani) in the second half of June. The rows were 24 in. apart and the rate was about 10 lb./acre. *Chloris gayana* (Tozi) was then broadcast by hand over the whole area. Both species remained yellowish and stunted on localized permanently flooded patches, totalling about 10 acres, which would best be planted to *Brachiaria obtusiflora*, but elsewhere growth was good and the area was grazed from late July onwards. Other promising legumes, including *Clitoria ternatea* (Tozi), are being tested with *Chloris gayana* on observation plots.

Acknowledgements. We are indebted to Dr. O. West, Mr. A. V. Bogdan, and Mr. H. J. Van Rensburg for supplying seed, and to the staff of the Herbarium, Royal Botanical Gardens, Kew, for naming sheets of the plants mentioned in this paper.

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THE MAURITIUS CREOLE BREED OF MILCH CATTLE

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With Plate 7

Summary

The Mauritius Creole breed of milch cattle is described; its history is discussed; and an account is given of the conditions under which the cattle are kept by the local peasants.

From experiments and observations at the Government Breeding Centre at Palmar, the Government Dairy at Curepipe, and on peasant-owned cows, it has been shown that this breed is superior in heat-tolerance to locally-bred Friesians and their crosses with the Creole breed, and that by improved feeding the level of milk production is capable of being increased to about double that obtained by the local peasants. About one-third of this increase is attributable to improved daily yield and about two-thirds to a longer lactation period. Data are presented regarding breeding efficiency, disease resistance, and health.

It is concluded that this breed, when improved and standardized by selection, may be capable of contributing materially to the improvement of dairying in the Tropics.

THERE is in Mauritius a breed of small-boned, unhumped, polled, rather under-nourished cattle, kept in some thousands of dark straw sheds in scattered villages among the trees, and owned by Indo-Mauritian peasants; it is a breed of unmistakably European origin whose history, until recently, was obscure and whose milk potential was unknown. This is the Mauritius Creole milch breed, usually referred to locally as the 'vache creole'. In 1951 there were approximately 32,000 of these cattle, owned by 17,400 people, or rather less than two per household. Of this total 26,700 were females (18,000 of breeding age) and 626 were mature bulls.

Apart from the Creole stock, and a few Friesians and their crosses with the Creole, there are also in Mauritius some 8,000 Zebu cattle originally brought in from Madagascar, East Africa, and India. Among these the Ongole type predominates. The Zebus graze for the most part on the coastal fringe of the island where they are kept on estates for the production of manure and for draught purposes.

It has thus happened, fortunately, that the two types of cattle found in Mauritius have been kept apart, and the Creole today provides useful material from which good milk stock can be bred for ultimate distribution all over the island. This is now the accepted long-term breeding policy for the improvement of milch cattle in the Colony.

Environment

Mauritius, an island of volcanic origin 716 square miles in extent, lies in the South Indian Ocean between longitude 57° 18′ and 57° 48′ east and latitude 19° 58′ and 20° 31′ south, i.e. about 1,200 miles from the east coast of Africa and just within the Tropic of Capricorn. The central plateau rises to 1,900 feet and is comparatively cool throughout the

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year. The coastal regions are warm from December to March when the mean air temperature is about 80° F. The south-east trade winds blow for most of the year and the climate is generally humid. The heaviest rains fall during the months of greatest cyclone activity—December to March—but on the central plateau there is no real dry season.

The average annual rainfall in the various parts is as follows:

East and south-east districts . . .	98·4 inches
Eastern slope of central plateau . . .	157·5 ,,
Central plateau	143·7 ,,
West and north-west	33·5 ,,

The annual average relative humidity varies from 70 per cent. on the west coast to 90 per cent. on the upper reaches of the plateau. Average air temperatures vary from 77 to 67·8° F.

Feeding

As four-fifths of the land devoted to agriculture is planted with sugar-cane, and food crops, tea, and tobacco occupy much of the remainder, there is little land available for pasture or forage crops. Most of the uncultivated land is forest or scrub.

The Creole cattle are owned by Indian peasants living in villages attached to sugar estates or on the fringes of towns where there are no grazing lands; for this reason and because of the presence of Stomoxys flies stall feeding is the general rule. In fact the cows are never taken out except for service or slaughter; and with the rapid spread of artificial insemination they will soon go out only for slaughter.

In the high-rainfall areas the most common grasses are *Ischaemum aristatum*, *Axonopus compressus*, *Panicum nossibense*, *Paspalum conjugatum*, and *P. scrobiculatum* var. *commersonii*. Of these, the first three are exclusive dominants. Growing in leached soil, all these grasses are of low nutritive value.

In the warmer and drier regions on and near the coast the main dominant grasses in the savannah and open country are *Heteropogon contortus*, *Themeda quadrivalvis*, and *Panicum maximum*, with *Stenotaphrum dimidiatum* forming a pure, dense sward in the Casuarina plantations along the narrow, sandy coastal belt. In these regions, *Leucaena glauca*, *Albizzia lebbek*, and *Litsaea glutinosa* also grow well and provide nutritious fodder.

In the medium-rainfall areas on the lower slopes of the central plateau, *Cynodon dactylon*, *Sporobolis* spp., *Paspalum* spp., and other grasses thrive between the canefields and are made use of by cow owners.

All fodder, collected for the most part by women, is fed green on the stable floor: sugar-cane tops in the cropping season (July to December) and, for the rest of the year, the grasses and shrubs already mentioned, plus handfuls of other nutritious and beneficial plants. Each cow with calf is given on an average two 70-lb. bundles a day, but much of this is wasted.

Before the First World War, when 'dholl' (pigeon pea) was cheap and issued by estates as part rations to their labourers, a pound or so per feed

was often given boiled to cows in milk with, it is stated, good results. Today this commodity is too expensive and where concentrates are fed they usually take the form of boiled Leucaena seeds in rice- and other vegetable-water. The efforts of the Agricultural Department to persuade cow owners to feed at least a modicum of balanced concentrates are meeting with fair success.

Calves are usually suckled after milking, the amount they get varying considerably. One survey put this quantity at 2·6 pints per day for the first 3 to 4 months.

Housing

The sheds in which the Creole cattle spend their lives are just large enough for them. Their construction is simple in the extreme, mainly cane straw on a frame of rough wood. The walls are from 3 to 5 feet high, the roof is pitched. The only apertures are a door usually at a side corner in line with the animals' heads, to facilitate feeding, and a small opening at the rear for the removal of manure to the adjoining pit. Both these openings are kept closed, usually with sacking, to exclude flies. The rough-cobbled uncemented floor slopes steeply to the back, the urine finding its way out as best it can. The warmth and humidity in such buildings in summer are considerable, but an appreciable amount of air no doubt percolates through the loose thatch and the occupants show no apparent signs of distress.

Description

The Creole is a small, neat, compact, polled, and humpless animal weighing when mature about 750 lb. The predominant colour is white or white with brown, dun, or dark markings. A brown or brown-and-white pattern is also met with. The colour patterns of 888 cows examined are set out below, and the measurements of sixty-seven cows are given in Table 1.

Colour Patterns of Creole Cattle	*Per cent.*	*Per cent. of total*
Pure white	16·6	
White with brown ears, eye-rings, or muzzles, or all three	5·6	
" " brown flecks, particularly on forequarters, head, and neck	8·6	
" " blue ears, eye-rings, or muzzle, or all three	2·1	
" " blue flecks, particularly on forequarters, head, and neck	5·0	
" " dun ears, eye-rings, or muzzle, or all three	2·8	
" " dun flecks, particularly on forequarters, head, and neck	3·5	
" " black ears, eye-rings, or muzzle, or all three	7·1	
" " black flecks, particularly on forequarters, head, and neck	11·5	
White and grey	0·1	
		62·9
All brown	8·3	
Brown and white	14·9	
		23·2
All blue roan	2·6	
Blue and white	6·3	
		8·9
Dun	1·6	
Dun and white	3·4	
		5·0

The skin is thin and creamy-white except where the hair is pigmented, when it conforms to the colour. The predominantly white coat colour is more the 'wild white' than the bright white of the white-spotted Friesian, and would appear to be a partial dominant. There are instances where three-quarter-bred and even seven-eighth Friesians with white Creole in their ancestry show no more black than eye-rings and ears or maybe blue flecking on head and neck.

TABLE 1. *Weight and Measurement of Creole Cows* (Average for Sixty-seven Cows)*

Weight	757 lb.
Height at withers	45 in.
Depth of chest	24·3 in.
Heart girth	63·7 ,,
Point of shoulder to point of pinbone	56·1 ,,
Width of hookbones	16·8 ,,
Width of thurls	15·1 ,,

* Most of the animals measured were out of condition. There are no figures for males or castrates.

Dun, although not common, appears to be very persistent. In the Government herd at Curepipe, there are a dun and a dun-and-white strain easily recognizable in the second and third generations from Creole. In some cases even the white-spottedness of the Friesian is suppressed.

All Creole cattle are naturally polled. The origin of this character is obscure and is referred to below. When crossed with Friesian bulls the progeny are all polled; about half the back crosses to Friesian are similarly polled.

In temperament these animals are placid and easily handled, while the cows let down their milk readily even in the absence of the calf.

As the Creole has no hump and shows no other signs of Zebu blood it may be considered to be pure *Bos taurus*.

History [1, 2, 3]

The origin of the Creole breed is obscure. The first cattle known to exist in Mauritius were in all probability Zebus or Sangas landed by the Portuguese after their discovery of the island in 1511. Many descendants of these were found by the Dutch, who made use of Mauritius as a victualling station during the sixteenth century, and were added to by similar importations. By the time the Dutch abandoned the island in 1710, however, practically the whole cattle population had died or had been destroyed. The French East India Company which next occupied and colonized Mauritius, then known as 'Isle de France', at once set about restocking with Zebus from Madagascar and India and with milk cattle from France shipped from l'Orient and other ports on the coast of Brittany.

Many references to the shipment of these cattle are to be found in the minutes of the Company, e.g.: '1745. It is especially recommended to

Messrs. La Chaise, du Desert the elder and Champelais to take every possible care of the calves and ewes which will be sent to them at l'Orient for shipment to Isle de France in spite of the difficulty which captains usually make in connexion with transporting these animals.'

From 1810, when the British captured the island, up to 1922, there are no reliable records of importations of breeding stock. Ongole, Mysore, and Hissar cattle, with a few Red Sindhi, were imported from time to time from India by sugar estates. A few importations of Shorthorn, Charollais, and Normandy cattle were also made, but these were too few to leave their mark. More recently, a few Afrikanders were introduced for use in the Zebu herds.

In 1922 a small consignment of about a dozen Friesian cattle was imported from South Africa in order to start a dairy herd at Curepipe; subsequently, in 1944, it was decided to cross Friesian bulls with the peasant-owned Creole cows, and in that year ten bulls were imported for this purpose. The extent of the dissemination of this blood was recently assessed by a survey of the colour patterns of Creole cows. Of 1,200 peasant-owned cows which were examined throughout the island, only 27 per cent. showed clear indications of Friesian blood.

The conclusion to be drawn from this historical survey is that the Creole cattle owe their origin to the introduction of French cattle from the Brittany coast during the eighteenth century. It seems possible that these animals carried genes for polledness, obtained from the old Scandinavian polled breeds. This is borne out by a letter to the Deputy Director of Agriculture, Mauritius, dated 2 November 1949, from Professor Lancelot of the Societé pour l'Equipement des Industries Laitieres et Agricoles, who quotes Professor A. M. Leroy of the Institut National Agronomique thus: 'Individual polled animals have been seen in France long ago, but were very few. Now there is not a single breed of polled cattle in France. We have only known in the last century the mongrel called Sarlabot which was created by mixing Normans and Red polled, so that it seems that if the herd in Mauritius is from Brittany, it is sure that later on polled animals have been imported into the Island.'

Many Creoles show the brown of the Normandy in varying amounts and the characteristic white face and eye-rings. L'Orient is not far from Normandy so that it is quite likely that some of the shipment from there consisted of animals of the Breton, Normandy, and Sarlabot breeds.

To go one step farther, Professor Ivar Johansson of the Royal College of Sweden in a letter dated 22 October 1949, to the Director of Agriculture about Swedish polled cattle, writes: '. . . cattle of this type have existed all over Northern Europe since the dawn of history . . . and have probably been rather numerous in the northern parts of the British Isles where fragments of this type exist. It does not seem unreasonable to suppose they have also existed in France in time past, although as far as I know there is nothing left of them now . . . We know that the Nordic Vikings in the period 800–1000 A.D. brought cattle over to England, and it is quite possible that they also carried cattle in their boats over to France where they made lots of raids along the coast.' Finally, Hammond [4] states: 'The primitive cattle of Great Britain and Ireland were

all horned, and Wilson has described how the various polled breeds of British stock were mostly derived from red stock brought over from Scandinavia by the Vikings.'

The writer originally attributed the white of the Creole to the Scandinavian Fjallras or mountain breed, but although Johansson merely mentions polled cattle, both Hammond and Wilson specifically state *red* polled cattle were taken abroad by the Vikings, presumably because the sea-rovers lived for the most part on the coast while the Fjallras were found farther inland. Furthermore, Leroy states that the Sarlabot was a cross between a red polled breed and the Normandy. There is therefore no obvious explanation of the origin of the white colour in the Mauritius Creole.

Breeding Policy

In view of the milk potential of the Creole and the complete acclimatization of the breed the Department of Agriculture has decided to make

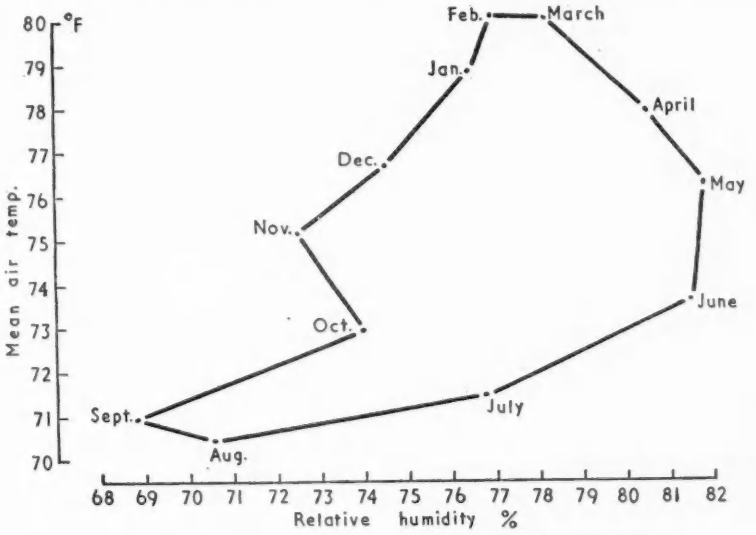

FIG. 1. Climograph of Palmar: March 1951–February 1954.

the fullest use of these cattle in its breeding programme. The first step in this programme towards the improvement of the Creole has been the establishment at Palmar Breeding Centre of a foundation herd which now consists of forty-three cows. Wherever possible they were selected in the field for high milk production. The cows are milked twice daily and are fed according to ordinary standards for milk yield. Twenty-two animals in all stages of lactation, many of them not yet in condition, are at present averaging 16·7 lb. of milk a day.

Concurrently, comparatively high-producing females are being sought

out in the field and milk-recorded with a view to their purchase for breeding purposes. These cows will be mated to the best available Creole bulls and their progeny, male and female, will provide material for selection within the breed. Eventually, progeny-tested bulls from high-yielding stock will be used in artificial insemination work over the whole island.

The 300-acre Stock Breeding Centre of Palmar is situated on the north-east coast at sea level. The appended climograph (Fig. 1) indicates the climatic conditions prevailing there.

Heat Tolerance

Tests were made over a period of 2½ months in the summer to compare the heat tolerance of Creole cattle with that of pure-bred Friesians and half- and three-quarter Friesian × Creole cattle. Except in the case of the halfbreds, four females were used in each group, two of which were in milk. Of the halfbreds, three were used, one in milk.

The procedure was as follows: Before being moved from the cool uplands to Palmar the temperatures of all fifteen animals were taken three times daily for a week to ensure they were all within the normal limits. The tests were started after allowing them two months in which to become accustomed to the new environment and constant handling. The period covered extended from 15 November 1951 to 31 January 1952, during which time the rectal temperatures of all the animals were taken on 38 days at 9 a.m., noon, and 3 p.m. Dry-bulb and relative-humidity readings were also taken daily at these times. Dry-bulb temperatures ranged from 80 to 87 with a mean of 84·5° F., relative humidity from 60 to 86 with a mean of 70 per cent.

The seven cows in milk remained throughout in an airy, thatched byre in which the dry-bulb temperature and the relative humidity approximated to within 1° F. and 1 per cent. respectively of readings from a nearby Stevenson screen. The dry animals were tied up in the sun on open grass at least one hour before each reading.

As it had been found that such relatively low humidities had little, if any, effect on rectal temperatures at Palmar, this factor was not taken into account; nor was air movement, as it could not be accurately determined. Since, however, this was a comparative test between genotypes under the same environmental conditions, the result was not affected by the exclusion of these factors.

The temperatures of the Creoles averaged 102·0° F. over the period; the half-breds 102·2° F.; the three-quarter-bred Friesians 102·6° F.; and the pure-bred Friesians 102·9° F. Still more significant is the fact that at a constant dry-bulb temperature of 87° F. (seventy-two readings for each of the four genotypical groups) the Creoles averaged 102·1, the half-breds 102·5, the three-quarter-breds 103·1, and the Friesians 103·6° F.

That there is a correlation between decline in milk production with increasing air temperatures and heat tolerance of the animals is indicated in Table 2, which gives the reactions of two Creole and two Friesian cows, all of which were at approximately the same stage of lactation and pregnancy.

In order to even out the normal variability of a cow's daily production, the 110 days covered by the test (14 October 1951 to 31 January 1952) have been divided into 5-day periods; the average of thrice-daily air-temperature readings and the average daily milk production per cow have also been similarly expressed.

TABLE 2. *Variation in Milk Production with Air Temperature*

Av. dry bulb temp. (° *F.*)		77	78	79	80	81	82	83	84	85	86
Creole	Av. daily prod. (lb. per cow)	18·4	18·5	19·0	..	17·2	16·8	15·4	14·7	..	12·8
	Variation in prod. (%)	..	+0·5	+3·3	..	−6·5	−8·7	−16·0	−20·1	..	−30·5
Friesian	Av. daily prod. (lb.) per cow	25·2	22·3	24·7	..	21·9	22·1	18·8	18·2	..	13·3
	Variation in prod. (%)	..	−3·6	−1·9	..	−13·1	−12·3	−25·4	−27·7	..	−47·2

Since there was an even increase in air temperature over the period under review as spring merged into early and mid-summer, the air temperatures are in chronological as well as numerical order.

Under normal conditions in the cooler uplands the average Creole cow could have been expected to show a 19·6 per cent. decline in daily milk production over the 110 days, a Friesian 16 per cent.

At the same time a third test was carried out with a wider range of genotypes using two dry, empty females of each. All animals were exposed to the sun on open grass for at least one hour before each of the thrice-daily readings. Mean dry-bulb temperature over the test period was 85·3° F. and relative humidity 70·3 per cent. Fifty rectal-temperature readings per animal were taken. The results are tabulated below.

TABLE 3. *Heat Tolerance Coefficients (after Rhoad) of Genotypes Tested*

Genotype	*H.T.C.*
Local *Zebus*	94·3
Ongoles recently imported from Madras	90·4
Creoles	89·0
Afrikanders. Bred locally	87·3
Halfbred Friesian × *Creole*	85·5
¾ *Friesian* ¼ *Creole*	82·0
Pure-bred Friesian bred locally	76·1

Although all the above were designed only as field tests, they may be taken as sufficiently accurate to demonstrate clearly the satisfactory degree of heat tolerance of the Creole and its superiority in this respect over the local-born Friesian and its crosses. Of the four Friesians used in the tests two were F2 from imported parents, one F3, and one F4.

Milk and Butterfat Production

Milk and butterfat recording has been carried out at the Government Dairy, Curepipe, for many years, but at the Palmar Stock Breeding

Centre only since the start of the Creole herd some three years ago. The herd at Curepipe consisted of Friesians, Creoles, and their crosses. Many of the records quoted in this paper are from both stations.

Unless otherwise stated, all yields of government-owned animals are for twice-daily milking and have been corrected for length of lactation (305 days), age (using J. F. Kendrick's tables), and pregnancy (using Sanders's figures as adapted by John Hammond, Jnr. [5]). In the light of experiment and observation it is certain that Creole females in poor condition recently purchased from Indian peasants are badly handicapped.

In 1951 six pregnant average Creole females were bought from Indians and calved down at Palmar. They were milked under conditions of housing and feeding closely approximating to those to which they had been accustomed as described above under 'Environment'. When dry and again pregnant five of these six animals (one had to be withdrawn on account of ill health) were transferred to an airy byre and brought into condition for a second lactation during which they were fed according to ordinary standards for milk production. In each lactation calves were removed at birth and the total milk yield recorded.

The results are given in Table 4:

TABLE 4. *Environmental Test with Creole Females*

Lactation	*No. of animals*	*Averages*			
		Length (days)	*Total milk (lb.)*	*Average per day (lb.)*	*Maximum per day (lb.)*
No. 1 .	6	192	1,366	7·1	13·4
No. 2 .	5	345	4,139	12·0	20·5
Percentage increase .	..	80%	203%	69%	53%

As will be seen later, the animals used in this test proved to be below average, but the results give a good indication of the extent to which the milk potential of peasant-owned Creoles is inhibited through malnutrition. There is no reason to suspect that improved housing contributed appreciably to the increase in yield.

Fifteen unselected Creole females, including the five used in the second part of the above test, all of which had belonged to the government for at least a year, averaged 4,342 lb. of milk in 305 days, or 14·2 lb. per day. The three highest producers gave 7,396, 6,800, and 5,174 lb. and the three lowest 2,713, 2,848, and 2,905 lb. Figure 2 shows the lactation curve of thirteen of these animals over a total of nineteen lactations averaging 11 months. The mean monthly (28 days) decline in milk production was 4·9 per cent. Figure 3 shows the comparative yields of the same fifteen unselected Creole females, locally bred Friesians from good South African stud stock, and Friesian/Creole crosses, most of them in the Curepipe Dairy herd but including a few Creoles at Palmar.

It is significant that the yield of the half-breds exceeds that of the Friesians, which shows, even when allowance is made for the possible beneficial effects of heterosis, that the Creole is not wanting in milk potential.

The yields of Creoles and their cross-bred descendants provide another basis for comparison. Six dams averaged 17·0 per cent. less milk

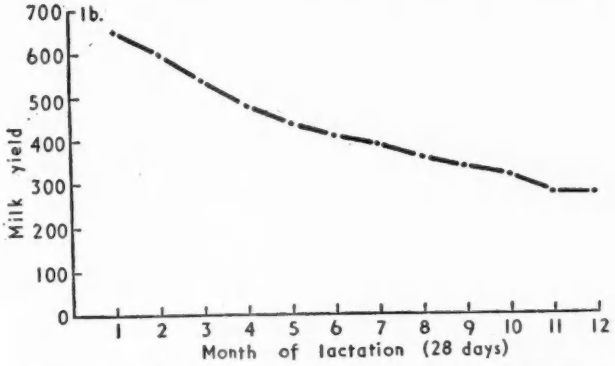

FIG. 2. Lactation curve of Creoles. Average of 19 lactations.

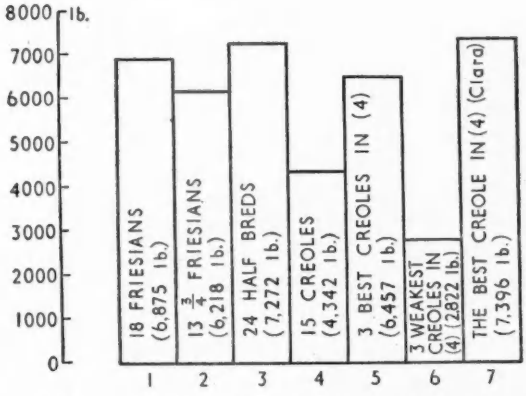

FIG. 3. Lactation yields of genotypes in herds at Curepipe and Palmar. 305 days corrected for age and pregnancy.

per corrected lactation than their twelve half-bred daughters and 7·3 per cent. less than five three-quarter-bred Friesian granddaughters, but one old dam (Clara) by producing 7,396 lb. proved herself to be a 22·7 per cent. higher yielder than her four half-bred daughters, none of whom came up to her level, and 31·9 per cent. better than two three-quarter-bred Friesian granddaughters.

Milk production of Creole cows in the field.—The assessment of yield,

length of lactation, and age at first calving among peasant-owned cows was not so simple a matter. Although it was realized that any figures arrived at could only be approximate, a certain degree of accuracy was essential if they were to be of any value. To ensure this three methods of assessment were employed, each one a check on the other two.

1. Three hundred and twenty cows in all stages of lactation were milk recorded one day a week for a month by the livestock officers, who also collected other relevant information.

2. The milk yields and length of lactation of ninety-four cows were ascertained through sales of milk to retailers, due allowance being made for the amounts consumed by the producers' families and the calves.

3. Under the supervision of the Animal Husbandry field staff, cow owners recorded the daily yields of 250 animals over a period of a month and submitted information about length of lactation, age at first calving, and amount of milk fed to calves.

As the findings of these three methods agree within reasonable limits they have all been made use of in arriving at the following means:

Number of samples	666
Average daily amount of milk drawn	9·94 lb.
Average daily amount of milk left in udder for calf[1]	0·93 ,,
Average total daily production per cow in milk	10·87 ,,
Average length of lactation[2]	201 days
Average total milk yield per lactation	2,185 lb.
Average monthly decline in production	7 per cent.

A comparison of these lactation yields of Creole cows in the field with those in the government herds clearly shows that the output of peasant-owned stock could be at least doubled by improved management alone, i.e. daily yield increased by 34 per cent. and length of lactation by 64 per cent. If three out of the comparatively few government-owned females recorded have been found to average 6,457 lb. per 305-day lactation, it is reasonable to assume that there must be many more with the same or even higher milk potential among the 18,000 cows on the island.

Butterfat.—Thirty-three government-owned Creoles averaged 4·04 per cent. butterfat over 224 tests covering all stages of lactation. There are no accurate figures for cows in the field. Auchinleck [6] found that the milk of seventy-one Indian-owned females on estates contained 3·74 per cent. butterfat, but it is known that among these were some carrying Friesian blood.

Breeding Efficiency

There is a high incidence of ovarian cysts among Creole cows due, no doubt, to lack of exercise. At the Government Dairy, where cows remain indoors throughout the year, 46 per cent. of breeding females have undergone enucleation of ovarian cysts in the past four years. In the field

[1] Equated to the total number of samples and spread over the whole lactation.

[2] That this short lactation is the outcome of environmental and not genetical factors is shown by the results of the feeding trial mentioned earlier and the lactations of government-owned Creoles.

13 per cent. of 11,000 females handled for artificial insemination were thus affected, but without a doubt many more which did not come on heat were not brought to the notice of the livestock officers. Fifteen per cent. of those inseminated returned, but it is certain that many more were not brought back, from mistrust of the new method of service in the early days of the artificial-insemination campaign. Where cattle are turned out to graze or for exercise, as at Palmar, no such trouble has occurred.

A survey of 500 cows in an intensively worked area gave a 75 per cent. conception rate after insemination. In the Government herd a mean of twenty-two Creoles over a ten-year period averaged 2·9 services per conception. This was before the problem of ovarian cysts had been methodically tackled. The other genotypes were no more fertile. With enucleation, the calving rate rose in three years from 65 to 82 per cent.

Age at first calving.—A survey of 198 females in the field gave the average age at first calving as 32½ months. The few Creole heifers in the Government herd have had their first heats well within two years of age, one being accidentally covered at fifteen months.

Calving interval.—Fifteen cows in the Palmar herd gave an average of 434 days between calvings.

Longevity and number of calves.—Too few samples are yet available to supply any data. Mention may be made of three cows of thirteen to fifteen years of age, two of which are still living and milking well. These three cows averaged ten calves each.

Disease Resistance and Health

Apart from tuberculosis and brucellosis there are now no major contagious diseases in Mauritius, and the peasant-owned Creole is usually healthy and singularly free from these. This may be attributed to the isolation in which the animals are kept. The rare instances of tuberculosis among Creoles are to be found only where a draught Zebu is a stable companion. Tuberculosis is very prevalent among these Zebus and among the Zebu herds run by estates on the coast. Brucellosis is confined to the Government Dairy at Curepipe, where it is now under control.

An analysis of some 10,000 cases attended by livestock officers over a period of 2½ years shows that the main causes of ill health were:

	Percentage of cases	*Percentage of bovine population per annum*
1. *Digestive disorders*	36·6	7·6
2. *Calcium and phosphorus deficiencies*	19·7	4·1
3. *Sterility* (ovarian cysts)	14·6	3·0
4. *Miscellaneous* (injuries, &c.)	12·5	2·6
5. *Udder troubles*	10·3	2·2
6. *Calving troubles*	6·3	1·3
7. *Tuberculosis*		NIL
8. *Brucellosis*		NIL
	100·0	20·8

Conclusion

In this paper an attempt has been made to give as complete a picture as possible at this stage of the Creole cattle of Mauritius. It may be concluded that this breed, when improved and standardized by selection, may be capable of contributing materially to the improvement of dairying in the Tropics.

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a

b

A typical stable in a village

c. A typical Creole in the Government herd

d. 'Clara', a 15-year-old Creole. 7,396 lb. of milk in 305 days

e. 'Clara's' half-bred Friesian/Creole daughter. 6,846 lb. milk in 305 days

f. The best $\frac{3}{4}$ Friesian/$\frac{1}{4}$ Creole cow. 9,461 lb. milk in 305 days

THE USE OF RESPONSE CURVES IN THE ANALYSIS AND PLANNING OF SERIES OF EXPERIMENTS WITH FERTILIZERS

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Summary

The estimation of the parameter k for average response curves of exponential form is briefly discussed and methods of estimating standard responses are examined. For these purposes the efficiencies of experiments of fixed size using different numbers of levels are compared and considerations affecting the design of experiments are discussed. The importance of the zero level is demonstrated.

In experiments with fertilizers the relationship between the yield of the crop and the amount of fertilizer applied is usually one of diminishing returns. As Stevens [1] has pointed out, a very large and accurate experiment would be required to decide between the various alternative forms of curve which might be fitted to the data. On general grounds, therefore, the exponential form of response curve, due originally to Mitscherlich, has been preferred to possible alternatives (e.g. polynomials) and has been found to be satisfactory, at least over normal ranges of fertilizer dressings. Crowther and Yates [2], Carey and Robinson [3], Yates, Finney, and Panse [4], and Hodnett [5] have used this curve in summarizing the results of large numbers of experiments, while Stevens [1] and Gomes [6] have considered its use in the analysis of single experiments. This paper discusses the applications of this curve in the analysis of series of experiments, the information provided by experiments with different numbers of levels on the response curve, and standard responses; and the implications for design.

The Response Curve

One form of the curve is

$$y = y_0 + d(1 - 10^{-kx}) \qquad (1)$$

where y is the yield obtained with an amount x of fertilizer, y_0 is the yield with no fertilizer, d is the limiting response, and k is a constant which determines the curvature of the curve (Fig. 1).

The main problem in using this curve lies in the determination of the parameter k. For this purpose experiments with three or more levels are required. In the simple case of dressings at three equally spaced levels Δx apart with yields y_0, y_1, y_2,

$$k = \frac{1}{\Delta x} \log \left(\frac{y_1 - y_0}{y_2 - y_1} \right) \qquad (2)$$

and the curve passes through the points. For four and five equally spaced levels Gomes [6] gives a simple method of successive approximations

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using tabulated values of certain polynomials. This method gives fully efficient estimates of k. He also shows how the residual variance (1 and 2 degrees of freedom respectively) may be calculated and how the curve can be used in the analysis of variance of a single experiment. Patterson [7] suggests simple direct methods of estimation for numbers of levels in the range 4–7. These estimates are not fully efficient (except in special circumstances), but in most practical situations there is little loss of precision. For example, with four levels the estimate

$$k = \frac{1}{\Delta x}\log\left(\frac{4y_2+y_1-5y_0}{4y_3+y_2-5y_1}\right) \tag{3}$$

has an efficiency of over 95 per cent. over the whole range, of practical interest, of values of the ratio given in brackets.

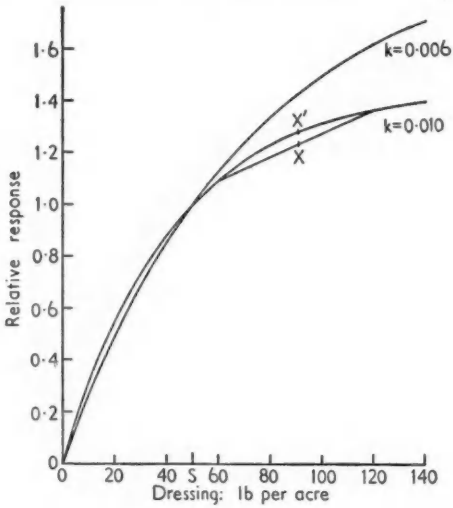

FIG. 1.

It is well known that the effects of fertilizers vary from place to place and season to season, so that the response curve may also be expected to vary. Consequently, when dealing with series of experiments it may appear desirable to obtain separate values of k for each experiment; but owing to experimental variation this is not always possible. Moreover, for most practical purposes, *average* response curves for groups of experiments are required. The value of k for such a curve is best determined from the mean yields for each level of fertilizer for the group, rather than as the average of separate k values. The latter is clearly unsatisfactory unless the experiments are very precise, since k has the value $\pm\infty$ in experiments with dressings at three equally spaced levels when y_2-y_1 or y_1-y_0 is zero and cannot be determined if these

differences are of opposite sign. Even with very precise experiments the mean of the k values will be biased. The determination of k is thus facilitated if the experiments are designed with uniform sets of dressings at equally spaced levels.

Standardization of Responses

In analysing responses to fertilizers, standardized responses are frequently required in order to combine information from experiments with different rates of application of fertilizers and with different numbers of levels. Using the response curve (1) the estimated response to a standard dressing s will be

$$r_s = d(1-10^{-ks}). \tag{4}$$

The response to any other dressing x relative to this standard response will follow the curve (Fig. 1) given by

$$R_x = \frac{r_x}{r_s} = \frac{1-10^{-kx}}{1-10^{-ks}}. \tag{5}$$

Table 1 gives the relative response curves for different values of k ($s=50$ lb./acre). For intermediate values linear interpolation may be used.

Having determined an average value of k, the standard response in experiments with only two levels is obtained simply by dividing the actual by the relative response. To assume that the response is directly proportional to the amount of fertilizer applied (as has frequently been done) is likely to give a misleading picture except for very low dressings.

With more than two levels of fertilizer, the standard response has been estimated in various ways. One way is to standardize the 'average' response, i.e. the difference between the yield of the untreated plots and the average yield of all the treated plots. This procedure clearly underestimates the standard response (cf. X, X' in Fig. 1), the magnitude of the bias for normal dressings being $2\frac{1}{2}$–$3\frac{1}{2}$ per cent. in experiments with three levels and 5–6 per cent. when there are four levels; it will therefore not be considered further.

Yates *et al.* [4], following Crowther and Yates [2], used the average of the standard responses—although the latter do not state how they estimated standard responses from experiments testing several dressings. This estimate is unbiased but is not fully efficient.

An equally simple estimate, which is fully efficient when k is known, is obtained as follows. By using equations (4) and (5) the response curve (1) may be written in the form of the linear regression of the yields y_x on the relative responses R_x:

$$y_x = y_0 + r_s R_x \tag{6}$$

in which the standardized response r_s is seen to be the regression coefficient. The required estimate is therefore

$$r_s = \frac{S\{y_x(R_x-\bar{R}_x)\}}{S(R_x-\bar{R}_x)^2}. \tag{7}$$

TABLE 1. *Relative Response Curves*

Dressing lb./acre	*k: acres per lb.*			
	0·004	*0·006*	*0·008*	*0·010*
10	0·238	0·259	0·280	0·301
20	0·456	0·484	0·512	0·540
25	0·557	0·586	0·613	0·640
30	0·654	0·680	0·705	0·730
35	0·747	0·769	0·790	0·809
40	0·835	0·851	0·866	0·880
45	0·919	0·928	0·936	0·944
50	1·000	1·000	1·000	1·000
55	1·077	1·067	1·058	1·050
60	1·150	1·130	1·111	1·095
65	1·221	1·188	1·160	1·135
70	1·288	1·234	1·204	1·171
75	1·352	1·293	1·244	1·202
80	1·413	1·341	1·280	1·231
85	1·471	1·385	1·314	1·256
90	1·527	1·427	1·345	1·278
95	1·580	1·465	1·373	1·298
100	1·631	1·501	1·398	1·316
105	1·680	1·535	1·421	1·332
110	1·726	1·566	1·442	1·346
115	1·770	1·595	1·462	1·359
120	1·813	1·623	1·479	1·370
125	1·853	1·648	1·495	1·380
130	1·891	1·672	1·510	1·389
135	1·928	1·694	1·523	1·397
140	1·963	1·715	1·535	1·404
145	1·997	1·734	1·547	1·411
150	2·029	1·752	1·557	1·416
155	2·060	1·769	1·566	1·421
160	2·089	1·785	1·574	1·426
165	2·117	1·800	1·582	1·430
170	2·144	1·813	1·589	1·433
175	2·169	1·826	1·595	1·436
180	2·193	1·838	1·601	1·439
185	2·217	1·849	1·606	1·442
190	2·239	1·859	1·611	1·444
195	2·260	1·869	1·616	1·446
200	2·281	1·878	1·620	1·448
210	2·318	1·895	1·627	1·451
220	2·352	1·909	1·633	1·453
230	2·384	1·921	1·637	1·455
240	2·413	1·932	1·641	1·457
250	2·439	1·941	1·645	1·458

This estimate may be written in the form $S(\lambda_x y_x)$ where the coefficients of the yields at the different levels are

$$\lambda_x = \frac{R_x - \bar{R}_x}{S(R_x - \bar{R}_x)^2}. \qquad (8)$$

The λ_x may be calculated for the different groups of experiments, after which the standardized responses are computed by the simple operation

of sums of products. An example of the computations is given in Table 2. No change in the procedure is required if the levels are not equally spaced.

TABLE 2. *Computation of Standard Responses*

Example: response of sugar-cane to phosphate: 50 lb. per acre P_2O_5
Average response curve, $k = 0{\cdot}010$ acres per lb.

Dressing (x) lb. per acre	R_x	$4R_x - S(R_x)$	λ_x	*Yield of sugar (y_x) tons/acre*
0	0·000	−3·103	−0·809	3·72
30	0·730	−0·185	−0·048	3·92
60	1·095	+1·278	+0·333	3·98
90	1·278	+2·010	+0·524	4·05
$S(R_x)$	3·103	$r_s = S(\lambda_x y_x)$	..	0·250
$4S(R_x^2) - [S(R_x)]^2$	3·834	$S(\lambda_x^2)$	1·042	..

Relative Efficiencies of Experiments of Fixed Size for Estimating Standard Responses and the Value of k

Since the standardized response may be given in the form $r_s = S(\lambda_x y_x)$ the estimated variance is

$$V(r_s) = S\{\lambda_x^2 V(y_x)\} \tag{9}$$

which reduces to

$$V(r_s) = \{S'(\lambda_x^2)\}\, s^2/r \tag{10}$$

if (as is frequently the case) the mean yields y_x have equal replication r, and s is the standard error per plot. For the example of Table 2, $V(r_s) = 1{\cdot}042s^2/r$.

TABLE 3. *Effect on the Variance of the Standard Response of Changes in the Number of Levels and the Range Investigated when the Size of the Experiment is Fixed*

Variance $\propto nS(\lambda_x^2)$

Range of dressings lb. per acre	*k = 0·006 acres per lb. No. of levels (n)*			*k = 0·010 acres per lb. No. of levels (n)*		
	2	*3*	*4*	*2*	*3*	*4*
0—						
30	8·64	12·93	15·28	7·52	12·30	13·44
60	3·14	4·62	5·60	3·34	4·83	5·84
90	1·96	2·88	3·48	2·44	3·45	4·16
120	1·48	2·16	2·64	2·14	2·85	3·52
150	1·30	1·80	2·24	2·00	2·58	3·20
180	1·18	1·65	2·00	1·94	2·40	3·00
210	1·12	1·50	1·80	1·90	2·31	2·96

The variance of a standardized response will thus depend on the rates of application, the number of levels, and the response curve. The effect of these factors is shown in Table 3, where comparable variances are given for experiments of fixed size. As expected, for a given number of levels greater precision is attained the greater the range covered, the rate

of change with range being greater in the case of the response curve with the lower value of k. Furthermore, for known k and a given range, experiments with two levels only give the lowest variance, but such experiments do not, of course, contribute to any estimate of the value of k.

The reduced precision of the estimates of the standardized responses in experiments with three and four levels is partly compensated by the information provided on the response curve. Table 4 shows the relative

TABLE 4. *Efficiency of Experiments with Four Levels Relative to Experiments of the Same Size using Three Levels for Estimating k*

Range of dressings lb. per acre	*Response curve*	
	$k = 0{\cdot}006$ *acres per lb.*	$k = 0{\cdot}010$ *acres per lb.*
0—		
30	0·91	0·91
60	0·92	0·97
90	0·96	1·09
120	1·02	1·26
150	1·08	1·46
180	1·18	1·73
210	1·28	2·21

information on the value of k to be obtained by increasing the number of levels from three to four in experiments of the same size. Only if the range is large will there be any worthwhile gain in precision. The actual gain in precision attained may be considerably reduced, unless the estimation of k is reasonably efficient, as, for example, by using (3).

Experimental Designs

In the planning of an effective fertilizer experiment decisions are required on the factors to be tested, the number of levels, the rates of application, the number of plots to be used, and the field layout, e.g. randomized blocks or Latin squares. With a co-ordinated series of experiments, reasonable uniformity of design and of the rates of application of the fertilizers is desirable in order to facilitate the analysis and combination of the results, while the organization of the field work will also be facilitated if the experiments are of approximately the same size and such that the teams are able to complete the various operations within one day. These elements in the planning are interrelated and are best resolved together.

For the simultaneous testing of a number of factors, standard factorial designs such as those given by Cochran and Cox [8] should be used. For general purposes, confounded designs of the types 3^n arranged in blocks of 9 plots and $4^p \times 2^q$ in blocks of 8 plots will be found to be most useful. If, for example, 27 plots are available, 3 factors each at 3 levels can be accommodated, thus providing an estimate of k—on which the information is rarely adequate—for each factor in addition to an estimate of the responses. Since it is natural to cover a somewhat greater range with 3 levels than with 2, there is not likely to be much loss in pre-

cision on the standardized responses as a result of including a third level. (See Table 3.) With 32 plots one factor at 4 levels and 3 each at 2 levels or 5 factors at 2 levels can be included. Thus factors at 2 levels will be useful when it is required to include more factors in an experiment of approximately the same size, as, for example, in a series of exploratory trials, while factors at 4 levels can be readily combined with others at 2 levels when information is required on the response curve for only some of the factors. Factors at 3 levels cannot be so conveniently combined with others at 2 or 4 levels since the confounding and analysis will be complicated.

The actual levels of each factor should be chosen to cover as great a range as is ever likely to be required in practice. The upper levels may well be uneconomic—and in that sense unrealistic—but their use will enable more precise estimates of the standardized responses to be made (cf. Table 3). By using the average standardized response and knowing the response curve and the prevailing prices of the crop and fertilizer, the optimal economic dressing may be determined, as illustrated by Finney [9] or Crowther and Yates [2].

When a crop responds well to a fertilizer, there may be little direct interest in the zero level, which is frequently considered unnecessary. However, failure to include this level may result in a substantial loss of information. Furthermore, the mean yield of plots without fertilizer is very useful in the interpretation of the results of the experiments, for a small difference in yield between two levels of application, neither of which is zero, may indicate a rapid falling off in response at higher rates or that there has been very little response under the experimental conditions. Similarly, if alternative forms of a fertilizer are being compared in the absence of the zero level, no clear difference in yield may imply no difference between the treatments or little response to either of them. Such uncertainties will be removed if the zero level is included.

Table 5 shows the reduction in the information on the standardized response when all the levels of an experiment are raised by the same amount. This reduction is independent of the number and spacing of the levels, being given by 10^{-2kx_0}, where x_0 is the lowest level. If, for example, all levels are increased by 20 lb. per acre, the information is reduced to 40 per cent. when $k = 0{\cdot}010$ acres per lb. and to 57·5 per cent. when $k = 0{\cdot}006$ acres per lb. One comparison of practical interest will be between an experiment with three levels, e.g. 30, 60, 90 lb. per acre, and one of the same size in which the zero level has been added. Using the data of Tables 3 and 5, with $k = 0{\cdot}010$ acres per lb., the relative variances of the estimated standard response from those two experiments will be $100/25{\cdot}1 \times 4{\cdot}83 = 19{\cdot}24$ and 4·16 respectively, so that the addition of the zero level increases the information by a factor of 4·6. If, however, the number of levels remains constant but the range is changed to 0–90 lb. per acre the information will be increased by a factor of $19{\cdot}24/3{\cdot}45 = 5{\cdot}6$.

Although it is particularly important in fertilizer experiments to include the zero level or as low a level as possible, insistence on the inclusion of this level of all factors in a factorial experiment may lead to

very low yields over a rather large proportion of the experiment. For example, if it is known that no response can be expected to phosphate and potash in the absence of nitrogen the inclusion of the zero level of nitrogen would be wasteful of one-third of a $3 \times 3 \times 3$ experiment. This undesirable situation can be avoided by using levels N_1, N_2, N_3 in the factorial scheme and adding extra N_0 plots in each block, so preserving the maximum information on the effect of nitrogen.

TABLE 5. *Loss of Information on Standardized Responses when all Levels are Increased by the Same Amount* (x_0)

Lowest level (x_0) *lb. per acre*	*Response curve*	
	$k = 0{\cdot}006$ *acres per lb.*	$k = 0{\cdot}010$ *acres per lb.*
	Per cent.	*Per cent.*
0	100·0	100·0
10	75·9	63·1
20	57·5	39·8
30	43·6	25·1
40	33·1	15·8
50	25·1	10·0
60	19·0	6·3
70	14·4	4·0
80	11·0	2·5
90	8·3	1·6

Although the precision of individual experimental results can be considerably increased by careful design and analysis, the major component of variation remains that between experiments. The precision of mean responses can be increased only by carrying out more experiments at representative sites and over a number of seasons. Sets of experiments of moderate accuracy, when considered as a whole, are thus of more value for practical purposes than a small number of isolated but highly accurate experiments from which it is often both difficult and dangerous to generalize.

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CAUSES OF VARIATION IN THE GESTATION PERIOD OF EGYPTIAN COWS AND BUFFALOES

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Summary

The aim of the present investigation was to study some of the factors influencing variation of the length of gestation in Egyptian cows and buffaloes. The average lengths for both sexes together were 289·0 and 318·7 days for cows and buffaloes respectively.

Sex of the calf had a significant effect on the length of gestation with cows but not with buffaloes. The average means for cows were: 289·8 for male calves and 288·2 for female calves; and for buffaloes 319·3 for male calves and 318·6 for female calves.

Birth weight of the calf in both groups of animals was significantly related to the length of gestation. Correlation coefficients between birth weights and length of gestation were +0·34 and +0·28 for cows and buffaloes respectively, which are statistically significant. Twin births shortened the length of gestation with cows; the average for single births was 289·9 and for twin births 283·8 days. This difference of about 6 days is highly significant.

The dam's weight and age significantly influenced the length of gestation in both groups of animals. Dam's weight and the gestation period increased gradually in both groups of animals to about 5–6 years old with cows and to 7–8 years old with buffaloes. Correlation coefficients between dam's weight and gestation length were +0·56 for cows and +0·27 for buffaloes.

The effect of sire was clearly shown in a significant influence on the duration of gestation with cows.

Month of calving did not have any effect on length of gestation for either cows or buffaloes.

STUDIES on the length of the gestation period as reported by Shrode and Lush [1] indicate that it is generally on the average 282 days for European breeds of cattle and 315 days for Asiatic buffaloes. Significant differences between breeds in the lengths of the gestation period, as frequently met in the literature, suggest that there is some genetic basis determining their length.

The duration of the gestation period in farm animals is of great importance to the animal breeder and dairy husbandman, for it is desirable that the dairy animal should be in a non-lactating state before parturition for a period between one and two months. Sources of variation affecting the duration of gestation in different breeds of cattle have therefore been investigated by many workers.

The present investigation was undertaken to study some of the factors that influence the length of the gestation period in Egyptian cows and buffaloes, viz. (1) Sex and sequence of calving; (2) birth weight of the calf; (3) weight and age of the dam; (4) effect of sire; (5) effect of month of calving.

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Materials and Methods

The data used in the present study were compiled from the records which have been kept on the Alexandria University Farm during the years 1942 to 1947. All the females were examined 2 months after service to record the exact date of service of the fertile animals. The gestation period for each animal was calculated from the time of fertile service to parturition. The method suggested by Lush [2] was used in estimating the number of days in the gestation period, i.e. the day in which the calf was born has been counted but not that of last service.

Pregnancies that resulted in stillborn calves or calves which died within a week from delivery were excluded from the present study. The number of gestation periods used was 180 (89 males and 91 females) for cows and 151 (81 males and 70 females) for buffaloes. Management and weighing of animals at different ages have been reported by Tantawy and Ahmed [3, 4].

Results and Discussion

Sex and sequence of calving.—Most workers, with various breeds of cattle, agree regarding the effect of sex on the length of the gestation period; males are carried a longer time than females [5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18], but some have failed to find any significant difference [19, 20, 21, 22].

In Egyptian cattle, Ragab and Asker [23] reported a significant difference between the sexes for buffaloes, but not for cows.

Regarding the effect of sequence of calving, several workers [10, 11, 12, 24] found significant effects of the calving sequence on the length of the gestation period, but other workers [e.g. 21, 25] reported no effect.

In the present study Table 1 shows the average length of gestation of males and females for both cows and buffaloes according to the calving sequences of their dams. With cows the average length of gestation of males was: $289{\cdot}8 \pm 2{\cdot}0$ and of females $288{\cdot}3 \pm 1{\cdot}5$ days; with buffaloes the length for males was $319{\cdot}3 \pm 2{\cdot}4$ and for females $318{\cdot}6 \pm 2{\cdot}2$ days. Males of both groups had longer gestation periods than females, the difference being 1·6 days for cows and 0·7 days for buffaloes, the former difference being significant.

The results reported here for cows agree with those reported for European breeds of cattle by various workers, but they show slight differences from those of Ragab and Asker [23]. These two authors recorded mean gestation periods for Egyptian cattle of 289·8 (males) and 289·2 (females), and 317·5 (males) and 315·8 (females), with cows and buffaloes respectively; the differences between sexes were significant for buffaloes but not for cows.

It can be seen from Table 1 that the differences between sexes increased gradually from the first calving to the fourth with cows, and to the fifth with buffaloes.

The method of analysis of variance for the expected subclass numbers

TABLE 1. *Numbers and Mean Length of Gestation Periods (days) in Cows and Buffaloes According to the Sex of the Calf and the Calving Sequence of the Dam*

Calving sequence	*Cows*					*Buffaloes*				
	Males		*Females*		*Difference*	*Males*		*Females*		*Difference*
	Number	*Mean*	*Number*	*Mean*		*Number*	*Mean*	*Number*	*Mean*	
1	18	288·3±2·2	23	287·1±1·9	1·2	14	317·4±3·9	15	317·0±2·3	0·4
2	13	289·6±2·5	21	287·9±2·1	1·7	11	318·6±1·6	11	317·2±3·2	1·4
3	12	292·0±2·0	11	291·3±1·6	0·7	12	318·9±2·3	14	319·5±1·5	−0·6
4	19	291·6±1·9	13	289·5±0·9	2·1	9	320·1±2·3	8	319·1±1·9	1·0
5	12	287·4±2·3	14	287·0±1·6	0·4	13	322·1±2·0	8	320·1±2·3	2·0
6 and over	15	290·1±1·2	18	286·7±1·2	3·4	22	318·0±2·2	14	318·4±2·0	−0·4
Total and means	89	289·8±2·0	91	288·3±1·5	1·6	81	319·3±2·4	70	318·6±2·2	0·7

3988.95

as suggested by Snedecor [26] was used for the effect of sex and sequence of calving.

Tables 2 and 3 show that the mean squares for sex is significant for cows but not for buffaloes. Sex × calving sequence interactions in both groups of animals are not significant.

TABLE 2. *Analysis of Variance of Gestation Period for Sex and Sequence of Calving in Cows*

Source of variation	*Degrees of freedom*	*Sum of squares*	*Mean squares*
Sex	1	182·20	182·20*
Calving sequence	5	224·30	44·86
Sex × calving sequence	5	53·30	10·66
Within individuals	168	7,265·20	43·25
Total	179	7,725·00	

* Significant at P = 0·05.

TABLE 3. *Analysis of Variance of Gestation Period for Sex and Calving Sequence in Buffaloes*

Source of variation	*Degrees of freedom*	*Sum of squares*	*Mean squares*
Sex	1	15·65	15·65
Calving sequence	5	264·09	52·82
Sex × calving sequence	5	33·58	6·72
Within individuals	139	8,333·20	59·95
Total	150	8,646·49	

Birth weight.—Studies of the effect of birth weight on the length of gestation have shown variable results. For European breeds of cattle [6, 7, 9, 27, 28, 29, 30] and for Egyptian cattle [3, 23] various workers have reported a highly significant correlation, while other workers [10, 15, 31, 32] found no significant correlation.

TABLE 4. *Correlation Coefficients (r) between Birth Weight and the Length of Gestation in Cows and Buffaloes (sexes averaged)*

	No. of calves	*Mean length of gestation (days)*	*Mean birth weight (Kg.)*	*r*
Cows	180	289·0 ± 1·8	26·2 ± 1·8	+0·34
Buffaloes	151	318·7 ± 4·5	40·1 ± 1·2	+0·28‡

‡ Significant at P = 0·001.

Table 4 shows the correlation coefficients between these two variables, for cows and buffaloes, in the present study.

These results demonstrate a highly significant correlation between birth weight of the calf and length of gestation in both groups, in agreement with most of the findings of previous investigators.

That twin births shortened the duration of pregnancy is claimed by various workers [5, 10, 17, 18, 24, 33]. Berger [34] reported a case of quadruplets with a gestation period of 258 days, this being 24 days less than normal.

The present study indicates (Table 5) that cows producing twins have shorter gestation periods than cows producing singles.

Table 5 shows that twin births shortened the length of gestation on the average by 6 days, the differences being highly significant statistically.

TABLE 5. *Average Gestation Periods for Single Births and Twin Births by the Same Cow*

	Single births (S)			
Cow no.	*No. of births*	*Average gestation period*	*Twin birth (T)*	*Differences (S–T)*
1	7	289·7±1·6	287·0	2·71
2	7	287·7±2·0	281·0	6·71
3	8	293·4±2·4	283·0	10·37
4	11	289·0±1·9	284·0	5·00
Total and means	33	290·0±2·0	283·8	6·19

Dam's weight and age.—Previous investigators are not entirely in agreement regarding the effect of the dam's weight and age on the length of gestation. Herman and Spalding [11] found a slight increase for mature cows, while other workers [7, 12, 19, 22, 35] reported no effect. Brakel *et al.* [6] found a significant difference of 1·46 days between the mean gestation lengths of cows 2 and 5 years old.

Table 6 shows the results obtained by the authors. Gestation periods increased gradually with age as well as with the dam's weight. Cows and buffaloes reached their maximum weights at the ages of 5–6 years and 7–8 years respectively. We may therefore conclude that when maturity in weight is attained, gestation periods cease to increase.

The correlation coefficients between dam's weight and the length of gestation, 0·5 for cows and 0·27 for buffaloes, are highly significant ($P = 0{\cdot}001$). One may conclude from these results that maternal factors (dam's weight and age) greatly influence the length of gestation. This influence could be attributed to genetic constitution and environmental conditions.

Effect of sire.—Several investigators [6, 22, 36, 37] working on European breeds of cattle, and Ragab and Asker [23] working on Egyptian cattle, all recognized the effects of the sire on the duration of gestation, while Burris and Blunn [7] reported that the sire had no effect.

Since only two buffalo sires were available in the present study, the influence of sires on the gestation period is discussed only for cows. Six sires were responsible for the largest number of gestations, and Table 7 shows the average lengths of gestation for calves by each sire.

The differences between the two extremes of mean gestation periods (8·4 days) is statistically significant as shown in Table 8.

These results show clearly that for cows the sire had a significant

TABLE 6. *Averages of Dam's Weight, Age, and Length of Gestation at Different Calving Sequences*

Sequence of calving	*Cows*				*Buffaloes*			
	Number	*Dam's weight (kg.)*	*Dam's age (years)*	*Mean gestation length (days)*	*Number*	*Dam's weight (kg.)*	*Dam's age (years)*	*Mean gestation length (days)*
1	41	389·4±7·7	3·29±0·07	287·7±2·3	29	533·0±15·5	3·88±0·44	317·2±2·3
2	25	426·3±12·9	4·22±0·12	288·7±1·6	22	573·4±17·0	5·30±0·49	317·9±4·1
3	23	448·0±13·6	5·28±0·13	291·7±3·3	26	598·8±21·0	6·30±0·18	319·2±6·6
4	32	426·3±13·5	6·46±0·04	290·6±1·2	13	642·5±16·6	7·40±0·23	319·6±2·3
5	26	433·2±15·9	7·30±0·24	287·2±1·4	21	628·7±22·2	8·95±0·26	321·4±5·6
6 and over	33	432·1±13·2	10·17±0·33	288·4±0·9	36	637·5±11·4	11·88±0·17	318·2±4·9

influence on the duration of gestation, which agrees fairly well with the results reported by other workers.

Effect of month of calving.—It has been reported that month of calving and seasonal effects have significant influences on the length of gestation;

TABLE 7. *Average Lengths of Gestation for Calves of Both Sexes by Each Sire*

Sire no.	*No. of calves*	*Mean gestation length (days)*
1	53	292·2±0·7
2	27	290·5±1·1
3	10	290·3±1·8
4	15	289·5±1·3
5	41	288·3±1·5
6	12	283·8±1·2
Total and average	158	289·1±1·3

winter freshening cows have longer gestations than those freshening during summer. Some workers [6, 11, 23, 24] showed significant effects for month of calving. Other workers [10, 12, 17, 30, 33, 38], however, obtained negative results.

TABLE 8. *Analysis of Variance of the Data Summarized in Table 7*

Source of variation	*Degrees of freedom*	*Sum of squares*	*Mean squares*
Between sires . . .	5	832·6	166·5†
Within sires . . .	152	6647·1	43·7
Total	157	7479·7	

† Significant at P = 0·01.

Most of the calves of the present investigation were dropped during the eight months from September to April. Table 9 shows the average length of gestation for both cows and buffaloes calving during the different months.

The longest gestation periods for both groups of animals occurred

TABLE 9. *Duration of Pregnancy for Cows and Buffaloes According to Month of Calving*

Month of calving	*Cows*		*Buffaloes*	
	Number	*Average gestation length (days)*	*Number*	*Average gestation length (days)*
September . . .	16	288·6±1·5	28	318·8±1·7
October . . .	39	290·4±1·1	22	317·5±2·7
November . . .	31	289·9±1·1	15	317·4±2·5
December . . .	38	289·8±1·2	24	319·3±1·4
January . . .	52	290·5±1·7	27	319·0±1·4
February . . .	17	291·8±2·3	27	320·9±1·2
March	9	292·4±2·5	24	319·2±1·5
April	14	290·4±1·6	12	318·8±3·0

during winter months. The differences between the two extremes are 3·9 and 3·5 days for cows and buffaloes respectively. These differences are not statistically significant, as shown in Tables 10 and 11. This could be explained on the basis that most of the calves were delivered during autumn and winter months when green fodders were available.

TABLE 10. *Analysis of Variance of Gestation Periods for Month of Calving in Cows*

Source of variation	*Degrees of freedom*	*Sum of squares*	*Mean squares*
Between months . .	7	145·3	20·8
Within months . . .	208	8793·4	42·3
Total	215	8938·7	

TABLE 11. *Analysis of Variance of Gestation Periods for Month of Calving in Buffaloes*

Source of variation	*Degrees of freedom*	*Sum of squares*	*Mean squares*
Between months . .	7	632·4	90·3
Within months . . .	171	15751·7	92·1
Total	178	15384·1	

Ragab and Asker [23] reported that month of calving had a significant influence on gestation periods for Egyptian cows and buffaloes, which is not in agreement with the results obtained in the present study. The question is whether this difference was caused by the differences in management and other environmental factors on the two farms or by genetic variability between the two herds; this needs further investigation.

Conclusions

Different factors that influence variation in the gestation period in Egyptian cows and buffaloes were investigated. The mean gestation period was 289·0 and 318·7 days (for both sexes) for cows and buffaloes respectively. The difference between the two groups of animals was almost a month, and in each group the gestation length fluctuated rather closely around each mean when pregnancy was normal. For cows gestation length of male calves was significantly longer than that of females, the difference being 1·6 days. For buffaloes the mean for male calves was 0·7 day longer than for females, which was not significant.

Birth weight and the length of gestation period had a significant positive correlation in both groups of animals. This does not mean that birth weight has a *direct* effect on the duration of gestation. Wright [39] states that any factor causing a delay in parturition should also cause an increase in the birth weight by allowing a longer time for the foetus to grow. It has also been shown from the present investigation that twin births shortened the mean length of gestation with cows, which was 283·8 days for twin births and 290·0 days for singles delivered by the same cows. This difference of about 6 days is statistically significant.

With buffaloes it was observed that twins were aborted at about 4–5 months of pregnancy.

The dam's weight and age showed significant effects on the length of gestation. One may infer, therefore, that maternal influences are the most important source of variation in the duration of gestation. Studies on Egyptian cattle reported by Tantawy and Ahmed [3, 4] and Ahmed and Tantawy [40] confirm these conclusions.

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THE VALUE OF LEAF-PROTEIN CONCENTRATES FOR GROWING AND LAYING PULLETS

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Summary

Pullets were housed in individual battery cages and fed on diets containing a single source of supplementary protein. Four experiments were carried out to compare leaf-protein concentrates with fish meal and groundnut meal in the diets of growing birds and laying pullets.

Leaf-protein concentrates were found to vary in nutritive value. The better ones were equivalent to fish meal for the *growth* of pullets from about 12 weeks old onward with relatively high protein diets.

None of the L.P.C. tested was as good as fish meal for *egg production* at high or low dietary levels. The feeding of 3 per cent. fish-meal crude protein, 5 per cent. groundnut-meal crude protein, and 5 per cent. lucerne-L.P.C. crude protein in a cereal diet resulted in a level of egg production substantially the same as that produced by higher levels of these concentrates. Egg quality was not adversely affected but L.P.C. caused a darkening of the yolk colour.

FRESH and dried grass are too bulky and fibrous to contribute much more than 20 per cent. to the total dry matter in normal poultry diets. If, however, the proteins of fresh herbage are concentrated by the methods described by Tilley, Barnes, and Raymond [1], then the resultant fibre-free leaf-protein concentrate (L.P.C.) can be used to replace the protein concentrates normally used in practical poultry feeds.

If the concentrate is prepared from lucerne (*Medicago sativa*), it is likely to contain a chick-growth-depressing factor which can be counteracted by adding cholesterol. Cowlishaw, Eyles, Raymond, and Tilley [2] have shown that this factor was present in some samples of lucerne and that the addition of cholesterol raised the 'gross protein value' (G.P.V.) of one sample from 57 to 74.

The amino-acid analyses of leaf-protein preparations by Lugg [3], Yemm and Folkes [4], and others show that, of the amino-acids essential in chick diets, only cystine+methionine is likely to be deficient. The nutritive value of L.P.C. for chicks has been measured by Cowlishaw, Eyles, Raymond, and Tilley [5] using the G.P.V. technique. They demonstrated that supplementation with methionine had no effect on the G.P.V. of a cytoplasmic leaf-protein concentrate in the absence of supplementary lysine, but it is probable that the heat treatment undergone by the L.P.C. during preparation had prevented some of the lysine from being liberated by enzymic hydrolysis. Supplementation of L.P.C. with lysine alone markedly improved the nutritive value of the poorer concentrates and slightly improved the nutritive value of the better concentrates.

Four experiments were carried out to determine the nutritive value of L.P.C. for growing and laying pullets. To obviate the possibility that

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the growth-depressing factor of lucerne might affect the nutritive value of lucerne L.P.C., cholesterol was added to all the lucerne-L.P.C. diets fed in Experiment 4 except one in which the L.P.C. had been washed with hot water.

Experimental

Rhode Island Red × Light Sussex pullets were used, housed singly in battery cages for each experiment. A minimum fourteen-hour day-length was maintained by means of electric lights. The birds were allocated at random to each treatment group after discarding those with extreme weights or with low previous egg yields. Flint grit, limestone grit, and water were available *ad lib.* to the birds at all times. All-mash diets were fed once daily either *ad lib.* (Experiments 1–3) or as a weighed quantity (Experiment 4). These mashes consisted of a mixture of ground cereals with the required vitamins and minerals added at adequate levels. The concentrate under test, or fish meal, or groundnut meal, was added to each diet except for a control diet in Experiment 4 containing no protein supplement. Mashes were mixed in small batches to last 8–10 weeks for Experiments 1–3, and in bulk and cold-stored until required for feeding for Experiment 4.

For Experiments 2 and 3 the concentrate contained material prepared from several different herbage cuts (lucerne, grasses, and chicory), but for Experiments 1 and 4 the concentrates were prepared from third- and second-cut lucerne respectively. The dry matter of the latter two crops contained approximately 3·6 per cent. nitrogen.

Experiment 1. A comparison of the weight gains, and age at sexual maturity, of growing pullets fed on diets containing a lucerne leaf-protein concentrate or fish meal.—Twelve-week-old pullets reared on a commercial mash diet were weighed and divided into two groups, each of fifteen birds. From 14 to 28 weeks old the pullets were fed a diet containing cereals, vitamin supplements (A, D_3, and B_2), minerals (2 per cent. calcium and 0·9 per cent. phosphorus), and either white-fish meal (10 per cent.) or lucerne L.P.C. (15 per cent.) to raise the total protein content of each diet to 16·4 per cent. crude protein (D.M. basis). Food consumption was measured and live-weights were recorded every 14 days. The number of eggs laid and the date on which laying commenced were recorded for each pullet.

Results are shown graphically in Figs. 1 and 2. No birds died during the experiment. The birds fed on the diet containing lucerne L.P.C. had a lower feed intake (11 kg. per bird) than those fed on the diet containing fish meal (12 kg. per bird) over the 14-week experimental period. Live-weight gains were not significantly different ($P<0·05$), but Fig. 1 shows that a difference in live-weight was established within the first 4 weeks. Sexual maturity, as measured by age at first egg, was delayed by one week. Egg yields were consistently lower from the group of pullets given lucerne L.P.C., the totals for the two treatment groups over 8 weeks being 17·0 and 24·5 eggs per bird. This difference may have been caused by the lower feed intake of those birds given the L.P.C. mash, and this in turn may have been due to the lower palatability of the lucerne L.P.C.

For egg production this sample of L.P.C. had a lower nutritive value than fish meal.

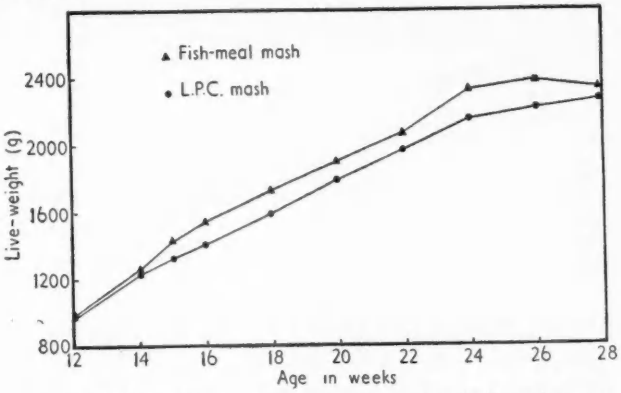

FIG. 1. Relation of live-weight to age for pullets in Experiment 1.

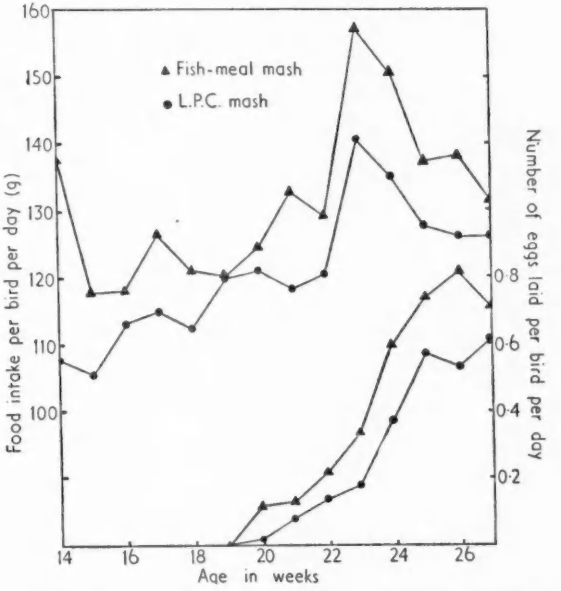

FIG. 2. Relation of food intake and egg yield to age for pullets in Experiment 1.

Experiment 2. The live-weight gain and food consumption of growing pullets on diets containing L.P.C., fish meal, or groundnut meal.—Ten-week-old pullets, reared on a diet of cereals plus either L.P.C. or white-fish

meal, were allocated to battery cages in a randomized-block layout. There were fourteen birds within each treatment group and six treatments. The diets fed to these groups were:

A. Basal mix + mixed L.P.C.
B. ,, ,, + fish meal
C. ,, ,, + groundnut meal
} Reared to ten weeks on cereals + L.P.C.

D. ,, ,, + fish meal
E. ,, ,, + groundnut meal
F. ,, ,, + fish meal and groundnut meal
} Reared to ten weeks on cereals + fish meal

The crude-protein levels of diets A to E were within the range 16·7 to 18·5 per cent. and that of diet F was 15·9 per cent. by analysis. Diet F contained two parts of groundnut-meal protein to one part of fish-meal crude protein. The phosphorus content of the diets was approximately 0·7 per cent. of the dry matter and the crude fibre approximately 7·5 per cent. The birds were allowed to balance their own calcium intake from the limestone grit available. Measurements were made of live-weight, food intake, and mortality. The experiment continued for 10 weeks.

The results are given in Table 1. No birds died during the experiment.

TABLE 1. *Live-weight Gain and Food Consumption (air-dry wt.) of Growing Pullets in Experiment 2 (per bird, 10–20 weeks old)*

Measurement	*Treatment*						*L.S.D.**
	A	*B*	*C*	*D*	*E*	*F*	
Initial live-weight (gm.)	688	671	694	1,053	1,046	1,037	36
Live-weight gain (gm.)	1,227	1,453	1,353	1,274	1,170	1,267	95
Weight gain %	178	217	195	121	112	122	..
Food consumption (gm.)	7,232	7,289	7,769	7,834	8,041	8,094	281
Mean age at first egg (days)	158	152	147	137	146	149	13

* Least significant difference (P = 0·05).

Those birds receiving fish meal in their mash (treatment B) made significantly greater gains in live-weight during the 10 weeks than those fed on L.P.C. (treatment A). Those fed on groundnut meal (treatment C) were significantly heavier than A and significantly lighter than B. When the chicks had been reared on a fish-meal diet to 10 weeks of age (D, E, and F), those subsequently under treatment D (fish meal) grew at the same rate as those subsequently under treatment F (fish meal + groundnut meal) and at a greater rate than those subsequently under treatment E (groundnut meal). Thus in both cases a fish-meal diet from 10 to 20 weeks old promoted greater growth than a groundnut diet. A 'resilience effect' was observed—birds reared on a medium diet to 10 weeks and then given a good diet subsequently gained at a greater rate than birds reared on a good diet and continued on a good diet. This is shown graphically in Fig. 3. Hammond [6] quotes work by Morgulis which demonstrated a similar effect with salamanders. The greater growth-rate of birds under treatments A, B, and C is paralleled by a lower food intake for treatments A and B and consequently better food utilization. The birds fed on the groundnut-meal mash (C) were able to maintain a high rate of growth only by eating more mash than was required

by the fish-meal-fed birds (B) for a slightly greater rate of gain. On the other hand, the birds given the L.P.C. mash did not eat any more food than the fish-meal-fed birds although capable of doing so. This was probably because the L.P.C. was less palatable than the groundnut meal.

The poor response by growing birds fed on the L.P.C. diet was probably owing to (*a*) the relatively low digestibility of herbage leaf proteins

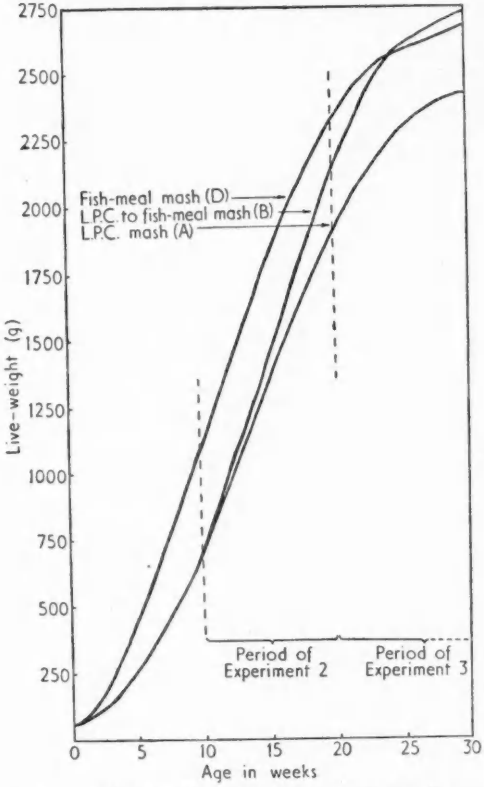

FIG. 3. The 'resilience effect' in growing pullets.

(Davies, Evans, and Parr [7]), (*b*) the lack of available lysine (Cowlishaw *et al.* [5]), and (*c*) the possible effects of saponins in the lucerne fraction of the concentrate.

The results of Experiment 1 differ in detail from those of Experiment 2. The periods over which measurements were made differed slightly between the two experiments and the L.P.C.'s which were used differed in origin. The lucerne L.P.C. used in Experiment 1 appeared to have a higher nutritive value than the L.P.C. of mixed origin used in Experiment 2; the former supported a rate of growth similar to that obtained by feeding fish meal.

Experiment 3. The egg production and food consumption of pullets fed on diets containing L.P.C., fish meal, or groundnut meal.—This experiment was a continuation of Experiment 2 using the same birds and the same treatments, except that the level of protein in the diets was raised by one-third. During the period 20 to 30 weeks old, the birds were weighed weekly and from then to 60 weeks old they were weighed every 10 weeks. Food intake was measured and recorded each week. Three birds died during the period 20 to 30 weeks old. At 30 weeks old the number of replicates was reduced to thirteen for each treatment by eliminating the poorest layer (or non-layer) from each of the other three groups at 30 weeks old. No other deaths occurred. A large sample of 530 eggs from treatments A and D was examined for yolk colour and greenish-tinged albumen. The date on which each bird started to lay was noted. The egg yields of each bird were recorded and each egg was weighed.

TABLE 2. *Live-weight Gain, Food Consumption (air-dry wt.), and Laying Performance of Pullets in Experiment 3 (per bird, 20–30–60 weeks of age)*

Measurement	*Treatment*						
	A	*B*	*C*	*D*	*E*	*F*	*L.S.D.**
Live-weight gain, 20–30 wks. (gm.)	473	604	506	326	474	516	149
Live-weight gain, 30–60 wks. (gm.)	443	542	472	515	487	628	150
Final live-weight at 60 wks. (gm.)	2,842	3,240	3,009	3,180	3,196	3,401	..
Food consumption, 20–30 wks. (kg.)	8·6	9·6	9·5	9·5	9·3	9·9	0·7
Food consumption, 30–60 wks. (kg.)	27·1	29·1	27·4	29·8	29·7	29·6	1·7
Mean age at first egg (days)	158	152	147	137	146	149	13
Number of eggs laid, 20–30 wks.	18	35	41	48	37	34	11
Number of eggs laid, 30–60 wks.	100	137	135	144	131	122	19
Mean egg weight, 30–60 wks. (gm.)	61·6	60·2	63·5	59·1	62·2	61·5	2·8

* Least significant difference ($P = 0.05$).

Results are given in Table 2. Live-weight gains were slightly greater within those groups (B and C) which had been fed on a L.P.C. for the first 10 weeks of life than within those groups (D and E) fed on a fish-meal mash over the same period. Group A fed on the L.P.C. mash put on more live-weight during the 20- to 30-week period than group D fed on the fish-meal mash, probably because sexual maturity had been delayed in group A. The final weight of group F birds, which had been given a lower-protein mash, was greater than that of any other group. Food consumption during the period 20 to 30 weeks old was similar for all the treatment groups except group A, which ate 9 per cent. less food than the other groups. During the period 30 to 60 weeks old, groups A and C ate 9 per cent. less food than the other groups, this difference being significant ($P < 0.05$). The difference between groups B and C was the reverse of that which occurred in Experiment 2 during the period 10 to 20 weeks old. Possibly the maintenance requirement of the birds under treatment C was less than for group B because their mature live-weight was 6·5 per cent. less.

By 30 weeks old, the effect of the two treatments imposed from birth to 10 weeks old was no longer measurable in terms of live-weight gain, food consumption, or egg yield. The differences in live-weight, which existed at 30 weeks old due to the six treatments imposed between 10 and 30 weeks old, were largely responsible for differences in the per-

formance of the pullets afterwards. By covariance analysis it was shown that the live-weight gains of the pullets from 30 to 60 weeks old were correlated ($r = 0{\cdot}412$) with food intake, and that this relationship was independent of treatment imposed (see Fig. 4). Another covariance analysis showed that the egg yield of the pullets was correlated ($r = 0{\cdot}412$) with food intake (see Fig. 5), but indicated that differences in egg yield between treatments were not wholly due to differences in food intake, evidence that the diets differed in quality.

From practical considerations it is certain that the relationship in Fig. 5 will be of a different nature when applied to a wider range of food-intake values. Egg yields will rise steeply as food intake increases from

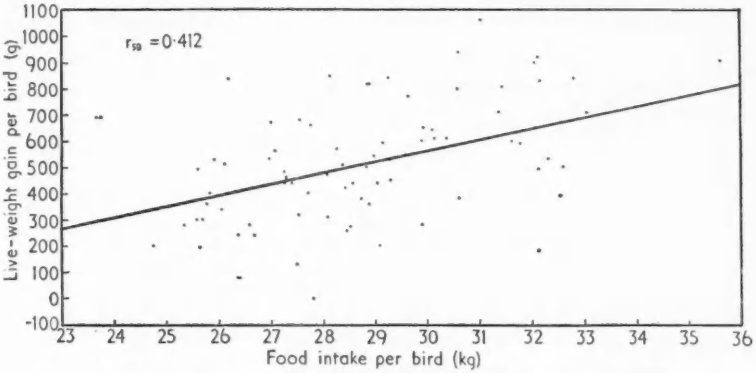

FIG. 4. Relation of live-weight gain to food intake of laying pullets over 30 weeks in Experiment 3.

about 12 kg. (about 60 gm. per bird per day) to about 26 kg. (130 gm. per bird per day). At about this value egg production will level off at approximately 150 eggs (70 per cent. production). The straightforward covariance analysis carried out on these data is incapable of showing such a non-linear relationship.

The average age at which laying started in group A was 10 days more than in groups B, C, E, and F and 20 days more than in group D, but comb development gave little indication of such differences. The number of eggs laid during the period 20 to 30 weeks old was least for group A and most for group D, the other groups being intermediate. The difference between groups A and D (18 and 48 eggs per bird) was greater than the difference which occurred in Experiment 2 between the group fed on the L.P.C. mash and the fish-meal-fed group (17 and 24·5 eggs per bird). The difference between groups A and D over the 30- to 60-weeks-old period was, however, of the same magnitude (44 per cent.) as in Experiment 1 over the period 20–28 weeks old. The production of eggs from 30 to 60 weeks old by group A was significantly less than that of any of the other groups, but there was no significant difference between groups B, C, D, and E. Group F laid fewer eggs than these groups probably because of over-fatness. The average weight of the

eggs laid by the birds within groups B and D (fish-meal mash) was significantly less than within groups C and E (groundnut-meal mash). Those birds fed on the L.P.C. mash (group A) or a mixture of groundnut and fish meal (group F) laid eggs of an intermediate weight. The eggs laid by birds given the L.P.C. mash had dark orange yolks, whereas from the other treatments the yolks were a very pale yellow.

In order to test the suggestion of Eyles [8], and Hughes and Eyles [9], that the greenish coloration of the albumen would cause green yolks on storage, half the eggs collected from treatment-groups A and D were

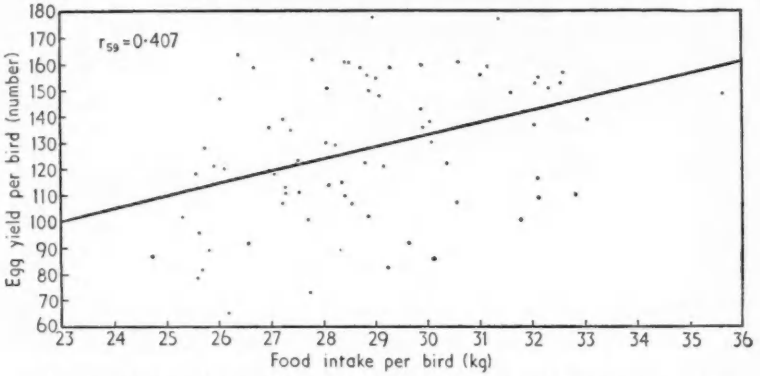

FIG. 5. Relation of egg yield to food intake of laying pullets over 30 weeks in Experiment 3.

stored for 12 weeks before being broken open. In none of the 265 eggs stored was a green yolk observed. The greenish tinge of the albumen was found to occur regularly in the eggs from a few of the birds under each treatment and never occurred in the eggs from other birds. Cruickshank [10] quotes Heiman as observing that the intensity of the yellowish-green pigment of the white of eggs was associated with the amount of riboflavin in the diet. Probably the same effect occurred in this experiment. Some birds evidently have a greater capacity to transmit this vitamin to their offspring than others. The yolk height in fresh eggs was not affected by any of the six treatments, but there was some indication that meat spots were more prevalent in eggs from birds with groundnut meal in their mash (C, E, and F). At the end of the experiment, eggs from groups A and D were again collected and opened in order to determine the manner in which the yolk pigments disappeared when L.P.C. was no longer fed. On average, nine more eggs had to be laid before the yolk colour was reduced to the same level as that of the yolks of eggs laid by birds fed on a fish-meal mash. The rate of disappearance did not depend on time but on rate of egg production, for one bird did not lay for six days and then produced an egg with a yolk as dark in colour as those produced whilst being fed on the L.P.C. mash.

Experiment 4. The laying performance of pullets fed on low-protein diets containing lucerne L.P.C., fish meal, groundnut meal, or no protein con-

centrate.—In previous experiments the diet was fed *ad lib*. and thus a further variable was introduced apart from weight gains and egg production. In this experiment each bird was limited to 120 gm. of mash per day. At this level all the food offered was eaten the same day except in a few cases of temporary sickness where the mash not eaten was fed back to the same bird at a later date in addition to her normal ration. Another factor tending to mask the difference in nutritive value between the three concentrates used in Experiment 3 was the high protein level of the mash. For this reason the protein levels in Experiment 4 were drastically reduced and a system was adopted similar to that used in 'gross protein value' trials with chicks [5]. A basal cereal mixture containing adequate levels of vitamins was incorporated into each diet in such proportion as to supply 8 per cent. crude protein in the dry matter (except in diet 5 wherein 10 per cent. crude protein was supplied by the basal mixture). Each diet was then balanced to contain 1·6 per cent. calcium, 0·8 per cent. phosphorus, and 7 per cent. crude fibre by using limestone flour, steamed bone flour, and oat food. The protein concentrate was added to supply 0, 3, 5, or 7 per cent. of crude protein (C.P.) to the dry matter of the diet. The concentrate used in each diet was as follows:

Diet 1. No concentrate—negative control.
„ 2. 3% C.P. from fish meal.
„ 3. 3% C.P. „ lucerne L.P.C.+0·3% cholesterol.
„ 4. 3% C.P. „ water-washed lucerne L.P.C.
„ 5. 3% C.P. „ lucerne L.P.C.+0·3% cholesterol (10% C.P. basal).
„ 6. 5% C.P. „ „ „ +0·3% „
„ 7. 5% C.P. „ „ „ +0·6% „
„ 8. 5% C.P. „ groundnut meal.
„ 9. 5% C.P. „ fish meal.
„ 10. 7% C.P. „ groundnut meal.

The lucerne L.P.C. was extracted from a crop of lucerne and meadow grass (*Poa trivialis*) cut at the end of August 1954 for the second time that year. The crop dry matter contained 90 per cent. lucerne and 3·6 per cent. nitrogen. The protein concentrate was prepared by the methods described by Tilley *et al.* [1] and was roller-dried. Part of this material was extracted with hot water at 70° C. and oven-dried. The mixed mashes were stored in water-tight bags at −10° C. to prevent deterioration. The experimental diets were fed from 8 weeks after the first bird commenced to lay. Those in lay by then, and not of very light or heavy weight, were allocated to the ten treatments and twelve blocks. The experiment continued for 16 weeks, during which egg yields were recorded daily. The birds were weighed at the start and finish of the experiment, and a sample of eggs from each treatment was opened to measure yolk and albumen colour.

Results are given in Table 3. The weight gains were higher for the 13 per cent. C.P. diets than for the 11 per cent. C.P. diets, and the negative control diet resulted in a small drop in live weight. The changes in weight were, however, very small. Egg production was at a low level (average 42 per cent.), partly owing to a failure in the battery house lighting system and partly to restricted food intake. From the results of

Experiment 3 it would seem necessary for pullets to put on weight if they are to lay at a high rate of production. Possibly a higher energy level in the diet would have permitted this to occur without any increase in dry matter consumption, but, as the diets contained an average of 20 per cent. maize starch, any increase in non-fibrous ingredients would have made the diets pasty and unappetizing.

The increase in fish-meal C.P. from 3 to 5 per cent. (diets 2 and 9) resulted in a small drop in egg production from 52 to 47 eggs per bird. With groundnut meal, the increase from 5 to 7 per cent. C.P. (diets 8

TABLE 3. *Live-weight Gain and Laying Performance of Pullets in Experiment 4 (per bird)*

Measurement	*Treatment*										*L.S.D.**
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	
Initial live weight (gm.)	2,350	2,248	2,406	2,355	2,374	2,253	2,295	2,231	2,415	2,331	..
Weight gain in 16 wks. (gm.)	−10	+39	+17	+78	+117	+78	+97	+102	+138	−7	..
Number of eggs	31·9	51·8	40·4	39·6	48·3	43·8	47·1	48·8	47·1	52·7	14·2
Mean egg weight (gm.)	54·5	60·6	57·1	58·8	61·6	60·4	63·6	58·7	60·4	58·0	..
Crude protein in diet (% in D.M. by analysis)	8·5	11·5	11·4	11·4	13·0	13·6	13·2	12·9	13·3	14·7	..

* Least significant difference ($P = 0.05$).

and 10) resulted in a small increase in egg production (49 to 53 eggs per bird). With lucerne L.P.C. the increase from 3 to 5 per cent. C.P. (diets 3 and 7) resulted in a rise in egg production from 40 to 47 eggs per bird. None of these changes was significant ($P < 0.05$), mainly because of the high coefficient of variability (37 per cent.) between birds within a treatment-group. With diet 5 (10 per cent. from cereals and 3 per cent. from lucerne L.P.C.), egg production was similar to that with diet 7 (8 per cent. cereals C.P. and 5 per cent. lucerne-concentrate C.P.), but, as 5 per cent. lucerne-concentrate C.P. was probably more than that necessary for maximum production, the two sources of crude protein are not weight-for-weight equivalent. Diet 4 (3 per cent. water-washed lucerne concentrate) resulted in an egg yield similar to that from diet 3 (3 per cent. lucerne-concentrate C.P. plus 0·3 per cent. cholesterol). When the diet contained 5 per cent. lucerne-concentrate C.P. plus 0·3 per cent. cholesterol, egg production was 44 eggs per bird, and when the cholesterol supplement was doubled it was 47 eggs per bird, a non-significant increase. Both levels of protein supplementation, except the L.P.C. (washed and unwashed) at the lower level and at the higher level with 0·3 per cent. cholesterol, caused a significant increase in egg production above that from the negative-control group (diet 1).

The mean egg weight was significantly lower from birds given the negative control diet than from the birds given the other diets. The yolks of eggs produced on the lucerne-L.P.C. diets were darker than any others, a result comparable to that of Experiment 3.

Discussion

The effect of feeding L.P.C. instead of fish meal in the diets of growing pullets was not the same in Experiments 1 and 2. In a further small-scale trial, Cowlishaw (unpublished data) fed one group of chickens on

a fish-meal mash and another on a lucerne-L.P.C. mash from 7 to 40 weeks old. The latter diet contained cholesterol to counteract the possible effect of any saponins present in the lucerne concentrate. The growths of the two groups during this period were not significantly different ($P < 0.05$). The mixed L.P.C. used in Experiments 2 and 3 evidently had a lower nutritive value for growth than the L.P.C. used in the other two experiments. The latter two lucerne L.P.C. supported rates of growth not significantly different from that obtained with fish meal, but the levels of crude protein in the diets (15 to 19 per cent.) were not critical.

Egg production was higher from birds fed on a fish-meal mash than from birds fed on a L.P.C. mash in all the experiments except when the lucerne L.P.C. was fed at the higher level with added cholesterol in Experiment 4. The difference in egg production between the two groups reared from birth on L.P.C. or fish-meal diets was 63 per cent. in Experiment 3 (groups A and D). Cowlishaw (unpublished data) found that the difference was 15 per cent. after 20 weeks laying using another L.P.C. When the pullets had been reared uniformly to 14 weeks old (Experiment 1) or to 10 weeks old (Experiment 3, groups A and D), the difference in subsequent egg production was 45 per cent. without added cholesterol. In Experiment 4, with added cholesterol, the difference was 30 per cent. when the concentrate supplied 3 per cent. C.P. and there was no difference when the concentrate supplied 5 per cent. C.P. in the dry matter of the mash. The counteracting of saponins by cholesterol may have had some effect on egg production, but the evidence is inconclusive.

It is evident from these results that the proteins from herbage have a lower value than those of fish meal for egg production, and this is probably mainly due to a lysine deficiency, shown by Cowlishaw *et al.* [5] to affect chick growth.

Carpenter, Duckworth, and Ellinger [11] found that the crude protein of grass had a nutritive value for chick growth equivalent to groundnut-meal C.P. and 60 per cent. of the value of fish-meal C.P. They showed that this was due to the low digestibility of the grass protein, and they also showed [12] that grass-meal C.P. was equivalent for egg production to groundnut-meal C.P. and barley-meal C.P. when each supplied 3 per cent. C.P. as a supplement to 8 per cent. cereal C.P. Their results compare closely with those of Experiment 4 both with regard to the relative egg production of birds fed on diets containing fish meal, groundnut meal, grass meal, or no supplementary protein, and to the smaller weight of the eggs from birds fed on an 8 per cent. C.P. diet.

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THE EFFECTS OF RESTRICTED INTAKES ON THE DIGESTIBILITY OF HAYS BY EAST AFRICAN HAIR-SHEEP AND ZEBU OXEN

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Summary

Studies are reported on the effects of restricted food intakes on six indigenous fat-tailed hair-sheep and ten local Zebu oxen, involving six different types of chaffed hay. Food intakes were varied from 60·7 to 182·5 per cent. of the maintenance hay ration in the different parts of the investigation.

No significant differences (at the P = 0·05 level) in digestibility coefficients nor in nutritive values were recorded when sheep were fed on chaffed hay at the maintenance level or at 75 and 80 per cent. of this intake.

With the oxen, significant differences (at the P = 0·05 level) were detected in the digestibility coefficients of the crude fibre fraction. The digestibility increased with a reduction in intake, the average values for sub-maintenance, maintenance, and super-maintenance rations being respectively 51·1, 50·3, and 49·4 per cent.

No significant differences in calculated nutritive values of the chaffed hays were found between the individual sheep or oxen used in these trials.

The starch-equivalent values of the hays did not differ significantly with the level of consumption in spite of the significantly greater digestibility of the crude-fibre fraction. There was, however, a general tendency for starch-equivalent value to decrease when the rate of consumption exceeded the maintenance level.

The values for digestible crude protein available from the hays increased at the sub-maintenance levels of consumption and, with two of the six hays studied, this trend attained a P = 0·05 level of significance.

BECAUSE local types of Zebu cattle and indigenous breeds of sheep so often exhibit a low order of productive efficiency under African conditions of management, it was considered desirable to ascertain the relative importance of certain management, nutritional, and climatic factors when these were operating in the absence of disease. A previous paper [1] has outlined the hard conditions under which cattle live in Masailand and has indicated the consequences of infrequent watering on digestive ability and nutrient intake when animals were living on a diet consisting solely of hay. The present contribution seeks to evaluate the effect of the even more ubiquitous factor of reduced fodder intake on digestive efficiency.

The problem of inadequate fodder consumption becomes most acute in the arid and semi-arid areas, where the dry-season need to secure water at a maximum practicable infrequency is balanced against the necessity of collecting the minimum of grazing necessary to maintain life. In such regions supplementary foods are not conserved and fed to the animals. In fact, except in certain restricted areas where contact with civilization has stimulated development, supplementary feeding is extremely rare in African herds in spite of the traditional custom of confining the animals in huts or open pens at night. This restriction at night might not be so serious a factor if the animals were able to graze in the early mornings and late evenings but, in the dry season, the stock often have to walk long distances to their grazing grounds. Furthermore,

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in the less arid areas where nomadism is not the normal practice, it is often customary for livestock to loiter in or around their night pens, without food, for up to one-third of the daylight grazing hours, before being herded on to communal and often over-grazed areas to collect their minimum of nutrient requirements.

The above examples of the inability of livestock in the sub-tropical areas to collect sufficient dry-season fodder are quoted to illustrate the widespread nature of the factors which inevitably lead to liveweight losses and to the seasonal reduction or cessation of milk yields.

Pasture utilization in other areas is seriously restricted by the presence of tsetse-flies, enzootic and epizootic diseases, or by the marked seasonal fluctuations in rainfall. Furthermore, the lack of adequate permanent water in certain areas severely restricts grazing habits and leads to overstocking in the vicinities of the permanent watering places. To those not familiar with local conditions, the annually recurring spectacle of overstocking, inadequate nutrition, and deaths from starvation appear paradoxical when considered alongside the equally distressing destruction of thousands of acres of grass by fire each year. While it is true that African herdsmen encourage fires in certain areas so that advantage may be taken of the subsequent young green grass shoots, it is unfortunate that lack of water and the presence of tsetse-flies preclude the use of even larger acreages of annually fired herbage. The African husbandman has not yet developed to the point where, in his opinion, the collection and cartage of fodders from such areas would seem justified. There is a marked reluctance to abandon existing tribal customs and, for many years, the majority of African-owned animals will continue to alternate between productive lush pasturage and subsistence dried-up herbage. Consequently, an understanding of the effects of underfeeding on digestive efficiency is of greater significance in such communities and conditions of husbandry than in more advanced countries.

The concern with the breeding, feeding, and management of improved livestock in the more advanced countries, where the bulk of research is centred, has inevitably led to the study of the economic productivity of rations which supply more than maintenance requirements. In those countries, few investigations have been designed to study such sub-maintenance subsistence as occurs annually under local African management conditions. This paper is therefore concerned with the consequence of restricted food intakes on the digestibilities and nutritive values of local dried herbage by indigenous Zebu cattle and hair-sheep. Apart from its intrinsic value for assisting African husbandry problems and livestock improvement schemes, this knowledge is of importance in connexion with the oft-asserted belief that imported exogenous stock possess digestive abilities inferior to those of indigenous animals and that this inferiority is a contributory cause of the failure of temperate breeds to thrive in tropical and sub-tropical environments.

Review of Literature

With the limited library facilities available, it has not been possible to make a full review of existing information on the effects of sub-

optimal dietary intake on digestive efficiency. A number of the references consulted concern the effects of reduced intake of mixed hay and concentrate rations, whereas the African system is concerned only with natural fodders unsupplemented with concentrates.

Henneberg and Stohmann [2, 3], who were the first to develop modern systems of food evaluation and rationing, based on digestibility investigations, recorded no substantial influence on digestibility due to the quantity of hay consumed. A similar conclusion was reached by Wolff [4, 5] a decade later from his experiments on sheep and horses. Muntz and Girard [6] likewise reported that the quantity of dry matter consumed by the horse exerted no significant influence on the digestibility of a lucerne-hay ration. In contrast with this earlier work, Armsby and Fries [7] found that, with steers, a sub-maintenance timothy-hay ration was somewhat better digested (1·0–2·7 per cent. on a dry-matter basis) than a maintenance ration of the same hay, although no appreciable differences had been detected in earlier studies on clover hay by the same authors [8, 9]. Kellner and co-workers [10] joined in this issue, and Kellner [11] clarified the position by pointing out that digestibility is unaltered by large or small rations when coarse fodders, unsupplemented with more nutritious foods, were the sole source of nutriment. His deduction that, when mixed rations of fodders and concentrates are fed, the larger ration is digested to a lesser degree has been confirmed by many subsequent workers.

This earlier work had been carried out using European types of animals, and the conclusions have been applied by analogy to the Zebu cattle and hair-sheep of the tropical and sub-tropical regions. Support for this implication is found in the comparative digestibility studies by French [12], which failed to demonstrate any significant differences in digestibility coefficients between Zebu and grade European oxen when feeding on the same Tanganyika hays.

Both before and since the publication of those results a number of writers, seeking to explain the known differences in productive efficiency or adaptability to hot environments, have postulated significant differences in digestive efficiency between indigenous Zebus and exotic grades and pure-bred animals. However, just as there is insufficient evidence [7, 13, 14] for concluding that, in *Bos taurus*, there is any significant difference in the digestive ability of different breeds or between pure-bred and unimproved animals so, in *Bos indicus* and its crosses with *B. taurus*, there is likewise no direct evidence to suggest that the Zebu possesses superior digestive powers. This is in line with modern views on the importance of micro-organisms in ruminant digestion. While considerable differences arise in the numbers and in the proportions of the various microbial species in the rumen, according to the type of food available, the cross inoculation of infusoria and anaerobic bacteria between animals feeding together renders it improbable that, in mixed herds, grade and pure-bred European animals would differ significantly in their rumenal microbial population from indigenous Zebus. With such an equivalence in rumenal micro-organisms it is difficult to visualize how the higher grade and pure-bred European

cattle could be at any digestive disadvantage, and it is more probable that their failure to thrive in tropical climates is due to environmental factors or to an impairment of the utilization or metabolism of digested nutrients.

A number of workers have been concerned in studying the comparative digestive efficiencies of cattle and sheep [4, 11, 15, 16, 17]. From such investigations it appeared that little difference occurred between the digestive powers of these two ruminants when the better qualities of roughages were compared but that cattle were the more efficient for the coarser fodders. This problem, as well as that of comparing the effects on digestive efficiencies of varying levels of intake, is subject to errors arising from slight variations in the digestive efficiency of a given animal at different times [18, 19, 20]. On the other hand, Christensen and Simpson [21], in a series of trials with lucerne hay, using four steers for two successive years, did not detect consistent individual differences between animals. Quite obviously, therefore, it would be inadvisable to base comparisons of digestive efficiency on single trials and, in the following studies, the results of several digestibility assessments have been analysed statistically.

Experimental Procedure

The trials to be reported were spread over 4 years and the procedure was, in each case, to chaff an amount of hay adequate for all the trials with a given set of animals. Unchaffed hay from the same stack was used for feeding during the pre-experimental and between-trial periods. Before the animals were placed on the metabolism crates they had been adjusted to the experimental intakes and had been on the unchaffed diet for from 15–20 days before being harnessed and put on to the corresponding chaffed hay. Faecal collecting periods varied in different trials from 10–14 days but, within any given series, the number of days for which faeces were collected was the same for all animals and levels of feeding.

In the first study, three pairs of local fat-tailed sheep were employed and were all fed with the same chaffed hay. In view of the possibility that different animals may exhibit slightly different digestive efficiencies, the later studies with oxen were planned so that a given pair of animals were used for the different rates of feeding. The aim in all studies was to feed a sub-maintenance ration and to compare its digestibility and feeding value with that of the same chaffed hay fed at about the maintenance level. In the oxen trials with hays 37N and 38N, a super-maintenance but not an *ad lib.* ration was fed whereas, with hay 37E, the third trial measured the effect of full consumption on digestive efficiency.

The analytical data concerning the compositions of the hays fed in the different trials are summarized in Table 1. From this it will be seen that the hays were typical of those produced in semi-arid areas of East Africa when *Cynodon plectostachyum* forms a high proportion of the herbage. The crude-fibre contents are lower than are recorded for less nutritive local grass hays but are higher than would be expected

in temperate areas. The crude-protein contents compare only with medium-poor British hays but are in accord with other figures published in East Africa.

Results with Sheep

Three pairs of typical Ugogo sheep, weighing between 45 and 49 lb. each, were fed simultaneously in this experiment. One animal of each pair was fed a maintenance ration of chaffed hay (35E) and the intention was to feed two of the remaining wethers at three-quarters of this rate and the remaining animal at the four-fifths maintenance level. In actual dry-matter consumptions, the quantities of hay fed to the three sheep

TABLE 1. *Dry-matter Compositions of Hays Fed in the Trials, per cent.*

Hay fed:	*Early cut hay (35E)*	*Early cut hay (36E)*	*Normal hay (36N)*	*Early cut hay (37E)*	*Normal hay (37N)*	*Normal hay (38N)*
Fed to:	*Sheep*	*Oxen*	*Oxen*	*Oxen*	*Oxen*	*Oxen*
Crude protein . .	9·53	9·47	8·68	7·53	7·26	7·51
Ether extract . .	2·02	1·82	1·51	2·09	1·11	1·08
N-free extract . .	43·56	45·46	42·39	42·98	43·19	45·53
Crude fibre . . .	34·70	33·62	37·66	36·70	38·44	36·77
Total ash . . .	10·19	9·63	9·76	10·70	10·0	9·11

on the restricted intakes worked out at 74·9, 76·9, and 80·1 per cent. of the amounts consumed by the corresponding animals on the maintenance diet. In Table 2 are given the average daily dry-matter consumptions by each sheep, the determined digestibility coefficients, and the calculated digestible-crude-protein and starch-equivalent values. No obvious differences were apparent and a statistical analysis failed to detect any significant variances between the digestive coefficients of the sheep fed at the different levels of dry-matter intake.

Results with Oxen

In the first trial with oxen, two pairs of animals were fed chaffed hay, 36E, at what was intended to be sub-maintenance and maintenance rates. Unfortunately, the quantity fed in the second case proved to be slightly below requirements and the series was repeated with hay 36N. In this second trial the quantity of hay fed proved to be approximately at the correct maintenance level and the dry-matter intake on the sub-maintenance diet was two-thirds of this amount. The results of these trials are incorporated in Table 3.

Calculation of the *t* values showed that, with these two hays and four oxen, no significant differences occurred in the digestibility coefficients for the organic-matter, crude-protein, and ether-extract components. The coefficients for the nitrogen-free extractives (43·7 and 43·1 per cent.) in the second trial (36N) were significantly lower (at the $P = 0.05$ level) for animals fed the maintenance ration but were not significantly different at the two sub-maintenance levels in the first series. In both trials, however, the crude-fibre constituent was digested significantly

TABLE 2. *Digestibility Coefficients, Digestible-crude-protein, and Starch-equivalent Values of Chaffed Hay Fed to Sheep*

Sheep no.	*Dry-matter intake/day (gm.)*	*Digestibility coefficients, per cent.*							*Digestible crude protein per cent.*	*Starch equivalent per cent.*
		Organic matter	*Dry matter*	*Crude protein*	*Ether extract*	*Crude fibre*	*N-free extract*	*Total ash*		
D	368·0	54·3	52·9	50·9	49·8	48·4	44·7	40·2	4·9	32·9
C	491·4	55·2	53·7	52·9	48·9	50·1	44·3	41·3	5·0	33·3
F	378·0	55·4	54·0	53·5	52·4	50·2	46·8	42·8	5·1	34·5
E	491·4	54·4	53·0	52·3	48·1	49·6	45·7	41·4	5·0	33·6
L	393·8	54·3	53·1	52·7	46·5	50·4	45·5	41·7	5·0	33·7
M	491·4	54·3	53·4	52·2	49·5	50·7	44·5	42·1	5·0	33·5
Mean maintenance		54·7	53·4	52·5	48·8	50·1	44·8	41·6	5·0	33·4
Mean sub-maintenance		54·7	53·3	52·3	49·6	49·6	45·3	41·6	5·0	33·7

TABLE 3. *Digestibility Coefficients, Digestible-crude-protein, and Starch-equivalent Values of Chaffed Hays Fed to Oxen*

Hay no.	*Ox no.*	*Dry-matter intake/day (gm.)*	*Digestibility coefficients, per cent.*							*Digestible crude protein per cent.*	*Starch equivalent per cent.*
			Dry matter	*Organic matter*	*Crude protein*	*Ether extract*	*Crude fibre*	*N-free extract*	*Total ash*		
36E	3	2693	50·2	52·3	56·3	56·5	57·6	47·4	30·9	5·3	38·1
	4	2693	50·9	52·9	57·3	58·4	57·6	48·4	31·4	5·4	38·7
	6	3590	49·9	51·9	55·2	60·8	56·2	47·7	31·1	5·2	37·9
	8	3590	50·0	52·1	55·1	56·5	56·6	47·9	31·1	5·2	37·9
36N	3	2685	43·8	45·1	58·4	54·9	47·7	43·8	32·6	5·1	31·9
	4	2685	43·5	45·0	58·5	54·2	47·4	43·6	33·6	5·1	31·8
	6	4028	44·0	45·6	56·4	55·8	45·5	43·0	30·0	4·9	30·6
	8	4028	44·6	46·0	57·8	58·2	46·0	43·2	31·7	5·0	31·1
37N	18	3157	44·7	46·4	49·8	47·0	49·2	44·2	25·6	3·6	31·2
	16	3157	44·8	47·0	49·7	46·3	49·5	44·3	24·9	3·6	31·4
	18	4059	44·4	46·4	48·3	45·2	48·5	44·3	26·1	3·5	30·9
	16	4059	44·1	46·2	48·5	47·3	48·1	44·0	25·4	3·5	30·7
	18	4961	44·0	46·0	48·0	46·2	48·0	43·9	26·6	3·5	30·5
	16	4961	43·5	45·7	47·4	45·8	47·7	43·5	24·3	3·4	30·2
37E	2983	2788	45·2	48·7	48·1	62·0	52·8	44·8	16·3	3·6	33·9
	3851	2786	44·8	47·1	48·2	65·9	50·5	43·1	25·6	3·6	32·4
	2983	4565	43·6	47·1	45·4	46·3	50·3	44·6	14·4	3·4	32·1
	3851	4589	45·2	48·1	48·0	56·9	51·4	44·9	20·6	3·6	33·2
	2983	5631	44·1	46·8	48·2	45·6	52·1	41·3	21·7	3·6	31·4
	3851	7574	40·5	42·5	43·0	49·7	47·1	38·0	22·6	3·2	28·0
38N	20	3150	46·5	48·2	51·1	47·3	52·7	44·2	28·6	3·8	31·4
	25	3150	45·3	47·3	51·3	50·0	52·0	43·5	25·3	3·9	32·9
	20	4050	45·6	47·4	50·9	48·2	51·9	43·7	27·2	3·6	32·8
	25	4050	45·3	47·3	50·0	48·8	51·5	43·3	25·3	3·7	32·5
	20	5400	45·2	47·3	50·5	47·4	51·2	43·5	43·6	3·8	32·6
	25	5400	44·7	46·6	50·0	47·2	50·5	43·0	25·1	3·8	32·0

better (at the P = 0·05 level) by the oxen on the lower level of rationing. (57·6 *v.* 56·4 per cent. for hay 36E; 47·5 *v.* 45·7 per cent. for hay 36N.)

The experimental procedure was again changed so that, in each of the three subsequent trials and unlike the above trials with sheep and oxen, a given pair of animals was studied at three levels of rationing. In the first series the rations were fed at approximately maintenance level and at 77·8 and 122·2 per cent. of this rate. In the third series the rates of rationing were maintenance and 77·8 and 133·3 per cent. of this amount. The position in the second trial was somewhat different in that the experimental oxen were of different sizes and the levels of rationing were, for Ox 2893, the maintenance rate and 60·7 and 165·0 per cent. of this intake. For the larger Ox 3851, the amounts of food consumed were approximately 67·2, 110·0, and 182·5 per cent. of maintenance needs.

The results of these three series of digestibility trials are included in Table 3. An analysis of variance shows that, with one exception, there were no significant differences in the digestibilities of the various food constituents by the individual oxen. This one exception occurred in the trial with hay 38N, when, as shown by the variance ratio test, Ox 20 digested the crude-fibre moiety significantly better (at the P = 0·05 level) than the corresponding Ox 25. (The variance ratio was 43·5 for $n_1 = 2$ and $n_2 = 2$.) Having established the relative unimportance, in this series, of individual variations between oxen, the digestibility coefficients for each pair of animals were averaged and comparisons made between levels of food intake and the types of hay being fed. Neither between hays nor between levels of consumption were any significant differences detected in the digestibility coefficients of the organic matter, ether extract, or nitrogen-free extract. For crude protein, different levels of hay intake did not give significantly different digestibility coefficients although the three hays differed significantly (at the P = 0·05 level) in the extents to which their crude-protein contents were digested. The variance ratio for P = 0·01 level of significance for $n_1 = 2$ and $n_2 = 4$ is 18, and the figure obtained (43·6) indicates significant differences in the digestibility of the crude-fibre moiety for different levels of hay intake. The differences between the digestibilities of the different hays were even more significant (at the P = 0·01 level when the variance ratio was 158·9).

From the digestibility coefficients of the individual animals and the crude compositions of the different hays, the respective nutritive values for the individual animals were calculated after deducting Kellner's correction factor of 0·29 for each percentage of crude fibre in the chaffed hays. This correction factor was used deliberately because only chaffed hays were fed and comparable results could not automatically be assumed for unchaffed fodders. The results are given in Table 2 for the sheep and in Table 3 for the cattle trials. In no cases were significant differences, in the digestible-crude-protein and starch-equivalent intakes, found between the individual animals in a given series, irrespective of the level of hay being consumed. Similarly, in the calculated starch-equivalent values, no significant differences at the P = 0·05 level were found as a result of limitations in the quantities of hay actually consumed

by the sheep or oxen. The starch-equivalent values of hays 36E and 36N, fed in the first oxen trials, differed significantly (when the variance ratio was 982 compared with the ratio of 167 required for $n_1 = 1$ and $n_2 = 3$ at the $P = 0{\cdot}01$ level), but no significance was found between the energy values of hays 37E, 37N, and 38N, used in the last three ox studies. In spite of this non-significant difference in the starch-equivalent values reference to Table 3 indicates that there was a tendency for the energy values to decrease on the super-maintenance diets.

The average values of the digestible crude protein in the different hays are summarized in Table 4.

TABLE 4. *Average Digestible-crude-protein Contents of Hays, per cent.*

Level of rationing	*35E*	*36E*	*36N*	*37N*	*37E*	*38N*
Sub-maintenance . .	4·99	5·38	5·07	3·60	3·62	3·84
Only slightly below maintenance . . .	..	5·22	..	..	..	..
Maintenance . .	5·0	..	4·96	3·52	3·52	3·64
Super-maintenance .	..	..	..	3·46	3·43	3·77

There are no significant differences in digestible-crude-protein contents between the different levels of intake for hays 35E, 36E, 36N, and 37N. Differences, significant at the $P = 0{\cdot}05$ level, were found in hays 37N and 38N and, except for hay 38N, the general tendency is for the digestible-crude-protein content to decrease with increasing consumption.

Discussion

The present studies with local sheep and oxen thus fall into line with observations made on European species. Many observations on European breeds of animals during the first half of the last hundred years suggest that digestibility of coarse fodders, fed unmixed with concentrated foods, is unaffected by the size of the ration. The present series of experiments on local sheep and Zebu oxen have also failed to demonstrate any appreciable changes in digestibility of the main food components, other than crude fibre, with variations in the level of consumption. For the fibre fraction, however, significant differences in digestibility were found, the smaller food intakes being associated with the higher digestibility. When, however, the starch-equivalent values are calculated, no significant differences were detectable between the energy value of the hays fed at the different intake levels in spite of the general tendency for energy value to be lower with the larger hay intakes. There was also a similar tendency for the digestible crude protein available from the hay to decrease with increasing quantities consumed and, for two out of six hays, this decrease was significant at the $P = 0{\cdot}05$ level.

It is obvious from these results that the effects of food shortage on digestibility and nutritive values are less significant than the consequences of water restrictions [1]. Restricted water intake reduces food consumption and the available digestible crude protein, so that the

tendency for an increase in the intake of the latter due to restrictions on food intake are more than counterbalanced by the effects of water shortage. On the other hand, in the case of crude fibre, water shortage augments the increased digestibility caused by the lower food consumption to the point where the starch-equivalent values of the hays consumed become significantly higher (at the $P = 0{\cdot}05$ level) when water is drunk only once in 72 hours. With more frequent watering the increase in the starch-equivalent values is, as recorded in this study on food restrictions, statistically insignificant.

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A NOTE ON THE RELATIONSHIP OF GAPS IN STAND AND YIELD OF DASHEEN

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UNDER Egyptian agricultural conditions it is difficult to obtain a complete stand of dasheen (*Colocasia esculenta*) owing to loss of corm-pieces by decay. The reduction in stand may amount to about one-third of the total number of corm-pieces planted, with resulting gaps in the stand. The plants adjacent to these gaps have more growing space and give bigger corms than normally spaced plants, which compensates in part for the loss in plant stand. The degree of compensation depends on the extent of gaps and competition between plants.

The relation of gaps of various length in the stand to yield of dasheen was investigated in this study.

Materials and Methods

Two experiments were carried out at the Experimental Farm of Alexandria University in 1953 and 1954. In 1953 the treatments were twelve single gaps, six double gaps, and four triple gaps per plot. The unit gap length was the space allowed to one plant in the row, 30 cm. The total gap length was thus the same in each treatment, i.e. 360 cm., or twelve missing plants per plot, representing a reduction of 12 per cent. of the full stand (100 plants per plot). In 1954, in addition to these three treatments, there was a fourth, consisting of a full stand of plants. The treatments were arranged in randomized blocks with twelve replications in 1953 and seven replications in 1954.

American dasheen (*Colocasia esculenta* Schott) was planted on 25 March and 1 April in 1953 and 1954 respectively. The distance between ridges was 87 cm. The plot size was 26·1 square metres in each experiment.

When the plants were about 25 cm. high, the required gaps of various length were made by removing plants from positions selected at random in the respective plots.

Results and Discussion

Some types of gap combination had a considerable effect on yield as shown in Table 1.

The yields of the different treatments were in descending order in each year as follows: twelve single gaps, six double gaps, and four triple gaps, with the full stand in 1954 giving a higher yield than any of the gap treatments. The difference between the single- and double-gap treatments was significant in each year; that between the double- and triple-gap treatments was significant in 1954 but not in 1953. The difference between the full stand and the single-gap treatment was not significant.

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In general, as would be expected, short gaps reduced the yield much less than the equivalent total space in longer gaps. The plants adjacent to long gaps did not grow sufficiently larger to compensate for the total loss in yield from reduction in stand. For the same total loss of stand,

TABLE 1. *Yield of Dasheen with Different Gap Combinations*

Gap combination	*Yield in tons per feddan*	
	1953	*1954*
Full stand	. .	14·22
12 single gaps	12·83	13·72
6 double ,, ...	11·11	12·20
4 triple ,, ...	10·55	11·14
Significant difference (P = 0·05)	1·39	1·01

the shorter the individual gaps the greater the number of plants able to benefit by extra growing space. Thus a 12 per cent. reduction in stand did not significantly reduce the yield when it was caused by no more than one plant being missing in any one gap.

This work emphasizes the importance of uniform stand of dasheen for commercial growers as well as in the conduct of field experiments.

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LEGUMES AND THE RHIZOBIUM SYMBIOSIS

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Summary

An examination of the evolution and present world distribution of species in Leguminosae suggests that the tropical legume is the typical one. The hypothesis is advanced that the cowpea type of nodule bacteria that is associated with tropical Leguminosae represents the ancestral condition and is the type of the genus Rhizobium. Rhizobium associated with such genera as Pisum and Trifolium is atypical in having a high requirement of calcium for growth. A suggestion is advanced for replacing the concept of the cross-inoculation group by a Symbiotic Rating. The need to appreciate the true position in the Rhizobium symbiosis for an intelligent development of leguminous pasture plants in the tropics is stressed.

THE history of our knowledge of the bacterial symbiosis in Leguminosae has been written almost entirely in temperate and cold-temperate regions of the earth. Furthermore it has been written largely in the northern hemisphere. Without attempting a detailed account the story may be stated briefly and broadly as follows.

Empirical knowledge of the soil-improving value of leguminous plants in agriculture extends back to ancient times, but it was not until 1886 that the mysterious nature of this beneficial effect began to be replaced by precise knowledge. In that year Hellriegel and Wilfarth in Germany, first showed conclusively by quantitative experiment that legumes are able to make use of atmospheric nitrogen unavailable to other plants. There ensued a great wave of interest in the subject. Beijerinck in Holland in 1888 was the first to isolate the bacteria from nodules and grow them in pure culture. They were then named *Bacillus radicicola*, but have subsequently been constituted a genus in their own right under the name of Rhizobium. Throughout Europe, in Germany, France, Italy, Holland, England, intense interest was taken in the subject in the following three decades, and many and varied aspects of the symbiosis were closely studied.

Following the 1914–18 war the focus of interest moved across the Atlantic to the United States of America where several influential centres of research on Rhizobium came into existence. The best known of these was, and still is, at Madison, Wisconsin. This centre is responsible for the two standard textbooks on the subject in the English language, by Fred, Baldwin, and McCoy [1], and by P. W. Wilson [2]. J. K. Wilson at Cornell, N.Y., came into prominence for his extensive studies on cross-inoculation phenomena and for his heretical views on the concept of cross-inoculation groups [3, 4, 5].

In the same period Virtanen and his co-workers in Finland roused great controversy on the subject of the excretion of nitrogen from the roots of growing legumes, and contributed much to the knowledge of the biochemistry of the nitrogen-fixation process. In England, at

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Rothamsted, Thornton [6] initiated a series of studies on variability of the bacteria, strain specificity in the host, and the physiology of nodulation. These studies have culminated in the ingenious work of Nutman [7, 8] that has made clear the dominance of the host plant in the symbiosis and the genetic control of its nodulating ability.

In very recent times southern Australia has come into the picture, starting with the pioneer work of Pittman [9]. Several centres of Rhizobium research are now active in Australia. Their work has been mostly confined to clovers and medics, perhaps the most significant contribution being the demonstration of the importance of molybdenum to the symbiosis of clovers [10]. Vincent [11] has effectively summarized Australian work.

From the beginning of research on nodule bacteria, investigators have been concerned, for very good reasons, with the legumes that grew and flourished under the climatic conditions with which they were familiar, and more particularly with the agriculturally useful species occurring in their immediate environment. The literature on the subject of nodule bacteria is consequently filled with references to plant species and genera characteristic of humid temperate and cool-temperate zones. Upon examination of any good selection of literature on the subject one is struck at once by the wealth of papers incorporating work on such genera as Trifolium, Medicago, Pisum, Vicia, Lens, Lathyrus, Lupinus, and by the corresponding paucity of papers on such genera as Vigna and Arachis. Amongst the latter group, papers in which cross-inoculation group studies are made account for most of the genera mentioned. When we come to examine the work on which is based what might be called our 'classical' knowledge of the Rhizobium symbiosis the field is very narrow. In 1952 in the *Proceedings of the Royal Society* appeared two review papers by Thornton and Nutman [12], as part of a symposium on symbiosis involving micro-organisms. They summarize succinctly our knowledge of the processes of infection and nodulation. An analysis of the literature cited in these reviews is shown in Table 1. References to the extensive cross-inoculation studies of J. K. Wilson [4] and to the book on the biochemistry of nitrogen fixation by P. W. Wilson [2] are omitted.

TABLE 1. *Analysis of Literature Cited by Thornton and Nutman* [12]

Number of papers cited	*Number of papers originating in each country*		*Number of papers dealing with the following genera*	
46	England	25	Trifolium	26
	U.S.A.	10	Pisum	17
	Finland	3	Medicago	10
	Scotland	2	Vicia	4
	Australia	2	Melilotus	1
	Canada	1	Lupinus	1
	Germany	1	Glycine (soybean)	12
	Holland	1	Phaseolus	3
	India	1		

The closer one examines the published work on the biology of the lugume symbiosis the narrower becomes the range of species used. The fundamental work on the biochemistry of nitrogen fixation by Virtanen *et al.* and by the Wisconsin group has been done very largely on Pisum, Vicia, Trifolium, and Glycine (Soybean) species. Our knowledge of the importance of the genetic constitution of the host plant in the symbiosis is due mainly to Nutman [7] working on red clover (*Trifolium pratense*), Aughtrey [13] working on lucerne (*Medicago sativa*), and Williams and Lynch [14] working on soybean (*Glycine max*).

The soybean is the only species possessing the cowpea type of Rhizobium on which a significant amount of work has been done.

The narrowness of our knowledge of the symbiotic relationship becomes more apparent if we examine what is known about the nodulation habits of the Leguminosae as a whole. Allen and Allen [15] and Allen and Baldwin [16] have summarized this knowledge. There are over 11,000 species recognized in the Leguminosae. Of this great array only about 1,200 have been examined for presence or absence of nodules. Botanists have proved singularly unhelpful in this matter. One would have expected that the possession of root nodules enabling the plant to exist in a condition more or less independent of soil nitrate supply would constitute a character as worthy of record as the possession of underground storage roots, or the presence of glands. None the less the taxonomic literature is almost devoid of reference to nodulation.

A point of great interest is that, of the 1,200 species that have in varying degrees been examined for nodulation, 133 or about 9 per cent. apparently never bear nodules at all. They thus lack entirely one of the most important characteristics that many people associate with Leguminosae. These 133 species are distributed in each of the great families in the following proportions to the number of species examined:

12/134 in Mimosoideae, 64/97 in Caesalpinioideae, and 57/969 in Papilionatae.

The number of species about which we have some knowledge grows steadily larger through the patient efforts of such workers as Bañados and Fernandez [17] who investigated the nodulation of ninety-one tropical species in the Phillipines, but a long time must elapse before we have even a rudimentary knowledge of a representative portion of the Leguminosae. In Australia, with a rich legume flora of between 1,200 and 1,300 species, there is published knowledge of the presence or absence of nodules on approximately 100 native species. At this point a word of caution is necessary. The absence of nodules even on a large number of plants sampled at one particular time is no guarantee that the species is a non-nodulating type. The work of Hannon [18] has clearly indicated that there may be a definite cycle of nodulation in perennial shrub and tree legumes. Observations were made on the following species growing on the Hawkesbury Sandstone soil near Sydney, N.S.W.: *Acacia discolor* Willd, *A. falcata* Willd, *A. oxycedrus* Sieb., *A. linifolia* (Willd), *A. juniperina* (Willd), *Dillwynia brunioides* Meissn, *D. ericifolia* (Sm.), *Pultenaea daphnoides* (Wendl.), *P. stipularis* (Sm.), and *Viminaria denudata*

(Sm.). Excavation of root systems at intervals throughout the year showed that in late summer and in winter (April–June) the great majority (80 per cent. approximately) of plants bore no nodules at all, in July approximately one-third of the plants were nodulated and in September all forty-five plants examined bore nodules. Should this type of cyclical nodulation be common to tropical legumes it could happen that the 'wet' season, when normally no one would go digging for nodules, might be the time of maximum occurrence, and the 'dry' season when digging is most likely to be indulged in, might be the time of minimum occurrence. This could result in a false picture of nodulating ability.

In view of the dearth of information on this subject it behoves those who write in general terms of the symbiotic relationship in legumes to preface their remarks with a caution. There is a widespread tendency to speak of 'legumes' when what is in mind is clearly 'clovers'. There can be no guarantee that what is true of clover is true also of the 10,000 species of legume that have still not been examined. If bacteriologists tend to generalize rather too widely in their discussion of symbiosis they may take comfort from the fact that agrostologists and agronomists are frequently more serious offenders. Their heritage is a knowledge of clover leys, and with them 'legume' and 'clover' are all too frequently synonymous. An example of this may be quoted from the excellent handbook *Legumes in Agriculture* issued by F.A.O. [19] in which appears the following statement (p. 87):

> Because legumes are invariably rich in nitrogen and independent of a low status of soil nitrogen, they are regarded as an especially useful and dependable source of protein for animal feeding.

And again on page 89:

> It is the unique chemical composition of legumes which gives them their great food value.

These statements are supported by data obtained on *Medicago tribuloides*, *Trifolium repens*, and *T. subterraneum*. One does not have far to turn to find that, if one really means 'legume' and not 'clover', then they are not 'invariably' rich in nitrogen, nor do they necessarily possess a 'unique chemical composition'. In the publication *Use of Legumes in Tropical Countries as Green Manure, as Cover and as Shade* [20] some analyses of legumes are given (p. 23) and there it is apparent that while many of the species examined are rich in nitrogen (*Indigofera endecaphylla* for instance has 3·09 per cent. dry-weight basis) at least one of them, *Mimosa pudica* with 0·97 per cent. nitrogen dry-weight basis, is lower in nitrogen than many grasses and other non-legumes. It is difficult to see why the 9 per cent. of leguminous species that have been shown not to bear nodules should possess a protein content greater than their non-leguminous associates since it is common knowledge that in species that can nodulate, the absence or ineffectiveness of nodulation results in a much lower protein content. Chemical analyses of these species would be of great interest if the information could be assembled. It is safe to say that, if we possess knowledge of the nodulating habits of only

10 per cent. of species in Leguminosae, we most certainly possess even less knowledge of their chemical composition, and are in no position to make generalized statements about the chemical composition of 'legumes'. It may be of significance that in his account of the browse plants of the Sudan, Harrison [21] notes (p. 21) that while leguminous species may preponderate in numbers there is nothing special about them that makes them better browse than plants of other orders and it is the species *Cadaba farinosa* (fam. Capparidaceae) that has the best reputation as a browse plant throughout wide areas of cattle country.

The Status of the Cross-Inoculation Groups

The concept of the cross-inoculation group was established quite early in the history of Rhizobium research. It was found that certain groups of plant species, closely related botanically, would nodulate with each other's strain of Rhizobium but not with strains from other plant species more distantly related botanically. For instance, Medicago species would nodulate with the bacterial strain from other Medicago species and from the closely related Melilotus and Trigonella, but not with other genera. Thus in course of time the groups were set up and since the work of Walker [22] it has become conventional to write them in the following order:

Group 1.	Lucerne	Medicago, Melilotus, Trigonella.
2.	Clover	Trifolium.
3.	Pea	Pisum, Lathyrus, Lens, Vicia.
4.	Bean	Phaseolus (in part).
5.	Lupin	Lupinus, Ornithopus.
6.	Cowpea	A great variety of genera covering the three families of Leguminosae and including part of Phaseolus.
7.	*et seq.*	A number of small sub-groups containing one or two species which do not fit into any of the other groups and are referred to as 'strain specific', that is, they will nodulate with their own peculiar strain of bacterium and no other.

The 'Cowpea Group' merits particular attention. Its title is fortuitous and appears to have had its origin in the work of Burrill and Hansen [23]. These workers found that a number of species in which they were interested had in common the property that their strains of Rhizobium would form nodules on cowpea (*Vigna sinensis*) and vice versa. Subsequently more species were referred by other workers to the 'Cowpea Group' of Burrill and Hansen and the title was launched in the literature. As it turns out many other species would have served as well as cowpea for a reference host. Wilson [3], for instance, found that *Crotalaria grantiana* cross-inoculated with a greater range of species than did cowpea itself. As time has gone on more and more species have been added to the 'Cowpea Group' until today it contains the great majority of those legumes that have been typed. Unlike the other cross-inoculation groups its members show the utmost botanical diversity possible within the limits of Leguminosae. From being a group it has passed to the status of an unruly mob. Within its diverse membership, however, interesting relationships can still be seen. For instance, it contains all

members of Mimosoideae and all members of Caesalpinioideae that have been typed. Within Papilionatae there are many temperate species included in its ranks but it is principally a repository for tropical species. The 'Cowpea Group' and 'tropical legumes' are strongly associated ideas. Allen and Allen [24] in Hawaii examined the cross-inoculation relationships of eighty-seven tropical species, native and introduced. All of these fell within the Cowpea Group.

There are inconsistencies within the Cowpea Group. Instances can be multiplied in which legume A will cross-inoculate with cowpea, and legume B will cross-inoculate with cowpea but legume A will not cross-inoculate with legume B. The soybean (*Glycine max*) provides an interesting example. Strains of Rhizobium from soybean will commonly nodulate cowpea, but only rarely will a strain from cowpea nodulate soybean. Inconsistencies are, however, not peculiar to the cowpea group. The work of J. K. Wilson at Cornell [3, 4, 5] has been treated with great reserve, amounting in some cases to frank unbelief, by orthodox workers on Rhizobium, and a certain amount of notoriety attaches to his attacks on the concept of cross-inoculation grouping as exemplified in his paper 'Over 500 Reasons for Abandoning the Cross-inoculation Groups of the Legumes' [5]. Nevertheless, a study of his published work reveals a careful and painstaking technique. To the best of the present author's knowledge, no worker has repeated his researches and published contrary results. In these circumstances one must accept his findings, no matter how disturbing to the established habit of thought, and make every effort to fit them into the picture. If one examines carefully the detailed data given by him (e.g. [4]) it becomes very evident that, provided a sufficiently wide range of bacterial strains is studied, no sharp boundary can be drawn for any cross-inoculation group, even such a homogeneous one as the clover group. To select an example, Wilson showed that a strain of Rhizobium from red clover (*Trifolium pratense*) gave excellent nodulation on the following species: *Amorpha fruticosa*, *Astragalus Cicer*, *Colutea arborescens*, *Desmodium polycarpum*, *Glycyrrhiza lepiota*, *Ononis vaginalis*, *Trifolium agrarium*, *T. fragiferum*, *T. hybridum*, *T. pratense*, *T. repens*, and *T. suaveolens*. This list includes species not only in different cross-inoculation groups but in different tribes of the Leguminosae.

In the early days of research on Rhizobium the cross-inoculation group served a useful purpose in rationalizing the problem of providing suitable strains of bacteria for commercial leguminous crops. Most of the species used in agricultural production in temperate regions fell nicely into one or other fairly clearly defined groups. This led to the conclusion that the clear-cut cross-inoculation group could be regarded as the normal condition in the Leguminosae. In actual fact, as will be made clear later, the well-defined cross-inoculation group such as the Clover Group represents an evolutionary cul-de-sac, and is atypical of the majority of Leguminosae. When this shall be clearly recognized then such cross-inoculation groups may have significance and value. But so long as they are believed to be the typical condition for the Leguminosae then they represent stumbling-blocks to progressive thought on the problems of host-bacterial relationships.

Rhizobium—the Bacterial Partner

It is, therefore, the more unfortunate that the present classification of Rhizobium as set forth in Bergey's *Manual of Determinative Bacteriology* should be based primarily on the cross-inoculation groups. Six species of Rhizobium (Fam. Rhizobiaceae Conn) are distinguished, as follows:

1. *Rh. leguminosarum* causing nodules on Lathyrus, Pisum, Vicia, and Lens.
2. *Rh. phaseoli* causing nodules on *Phaseolus vulgaris*, *P. multiflorus*, and *P. augustifolius*.
3. *Rh. trifolii* causing nodules on Trifolium.
4. *Rh. lupini* causing nodules on *Lupinus* spp. and *Ornithopus sativus*.
5. *Rh. japonicum* causing nodules on *Glycine max* (soybean).
6. *Rh. meliloti* causing nodules on Melilotus, Medicago, and Trigonella.

In this the pattern set by Garman and Didlake [25] is followed fairly closely. These authors, without the formal blessing of a Latin binomial referred to 'the alfalfa nodule organism, the clover nodule organism, the vetch and garden pea nodule organism, the cowpea nodule organism, the soybean nodule organism and the garden bean nodule organism'. The lupin species, which Garman and Didlake did not study, has been inserted, and it is noted that, although no name is given to the cowpea organism, its identity with the soybean organism is very probable. The paradoxical nature of this latter note will be made clear later.

Many workers have discussed the species relationships of the genus Rhizobium after detailed study of many strains. Some have decided that they show sufficient differences to constitute separate species, but others have decided that the differences between them are only of the magnitude of strain variation within a species. The fact that such a large element of subjective judgement can enter into the matter is sufficient to indicate that with the techniques available today there can be no final basis for species differentiation. It is, therefore, difficult to see any advantage to be derived from artificially classifying these organisms into species as they are constituted at present.

Within the mass of controversial fact on this subject, as within that on the Cowpea cross-inoculation group, we can, however, discern broad relationships that may have significance. Burrill and Hansen [23], who supported the one-species concept, studied the cultural characters of isolates of Rhizobium from fifty-nine plant species. They found that when grown upon ash-agar slants the cultures could be divided into three groups which they described as follows (p. 139):

> Group I. The organisms are distinguished by the thin scant growth upon the slant; the streak is a dull grey-white. They are exceedingly slow growers, colonies on agar plates being especially slow. They are not sticky to the touch, and spread quite easily in water upon the cover slip. Flagella are quite easily demonstrated, since there is little gum to interfere. The group includes *Vigna*, *Cassia*, *Acacia*, *Lespedeza*, *Desmodium*, *Baptisia*, *Genista*, *Arachis*, *Mucuna*, *Glycine* and *Amphicarpa*.
>
> Group II. The organisms of this group grow more rapidly than those of Group I. The growth is moderate to abundant with but little tendency to spread. The streak is raised, glistening opaque, and pearly white in colour. Though not very sticky to the touch, there is considerable gum, which seriously interferes in attempts to stain flagella. *Melilotus*, *Medicago* and *Trigonella* make up this group.

Group III. The growth of these organisms is very fast, and there is a strong tendency to spread. The streak is watery and semi-translucent, being quite different from the opaque growth of Group II. The surface is not so shiny as in that Group. Further, the organisms are quite slimy and usually quite sticky to the touch. The excessive amount of gum prevents staining of flagella and holds the organisms in clumps so that they cannot be spread easily on the cover slip. The organisms of *Vicia*, *Pisum*, *Lens*, *Lathyrus*, *Trifolium*, *Phaseolus* and *Strophostyles* are included in this Group.

Conklin [26], though she did not study any plant species yielding bacteria falling into their Group II, agreed in dividing her isolates into two very definite groups coinciding with their Groups I and III. Her Group I included 20 cultures from *Amphicarpa bracteata*, 24 from *Baptisia tinctora*, 27 from *Cassia nictitans*, 5 from *Crotalaria sagittalis*, 10 from *Desmodium paniculatum*, 9 from *Genista tinctoria*, 3 from *Lespedeza hirta*, 2 from *L. frutescens*, and 2 from *Dolichos lablab*. Her Group II included 3 cultures from *Lathyrus latifolius* and 13 from *L. japonicus*. Great detail of the cultural characterization of these groups is given.

Conklin was at pains to point out the almost indefinite range of minor variation that may be expected within a group and this picture has been confirmed by many subsequent workers.

The broad grouping of Rhizobium strains on their cultural characteristics seems to be further supported by data obtained on their serological reactions, and on their susceptibility to phage attack [27].

It could be that these groups represent a sorting of Rhizobium into distinct evolutionary types, but their significance is at present obscure. It is particularly puzzling when strains of bacteria that fall into two of the groups are obtained from plants within the one genus, as was found, for instance, by Johnson and Allen [28] in Sesbania.

The Origin and Distribution of the Order Leguminosae

With knowledge of the cross-inoculation habits of bacterium and host, and of the specific status of the bacteria, in a state of indecision, it is important that other avenues of thought should be explored in an effort to understand better the problem of symbiosis. One of these avenues that might be expected to lead to some understanding of the problem but which has been almost entirely neglected is an inquiry into the botany, both past and present, of the Leguminosae. This great Order had its origin, according to Gundersen [29], in upper Cretaceous times when with a tremendous upsurge the Angiosperms came to dominate the earth's flora, and many modern dicotyledonous families became well established.

A neglected paper that is nevertheless of great importance was presented by E. C. Andrews to the British Association for the Advancement of Science in 1914 [30]. Andrews makes clear the nature of the environment to which the early Leguminosae were subject in Cretaceous and early post-Cretaceous times.

Modern geography is characterised by the presence of high mountains, great deserts, large continents, small inland seas, glaciated poles, and a strong differentia-

tion of climate generally. Upper Cretaceous geography, on the contrary, was characterized by the presence of low-lying lands, by large epicontinental seas, by an extension of mild and genial climate from the tropics to the polar regions. The fossil plants discovered in sediments of this age suggest, moreover, that the climate was moist as well as mild.

The general lack of relief in the Cretaceous continents appears to have been due to the action of long-continued erosion, while the great epicontinental seas were caused by a general rise of the ocean levels, suggestive of a spilling over of the oceans basins on to the continents. North America was separated thus into two portions by a long and wide sea running north and south from the Gulf of Mexico to the Arctic Ocean. A great Mediterranean sea appears to have extended from the Mexican Gulf right across Southern Europe and Northern Africa, to the Eastern portion of the Himalaya. Australia also was almost completely separated in two portions by a long and wide sea extending southwards from the Gulf of Carpentaria. The continents of Asia and Africa also appear to have been isolated towards the close of the Cretaceous by the general rise of the water in the ocean basins.

Andrews argues convincingly that the Order Leguminosae established itself in the tropics at this time when the tropical regions of the continents were interconnected. Since the great land blocks were separated from each other near the close of the Cretaceous, differentiation of the legumes has gone on separately in each of the continental blocks. At the present time the legume flora of each continental block, though obviously related to that of the other blocks, is nevertheless characteristic. Thus, for instance, the Acacias of Africa constitute a group with close affinities, and the Acacias of Australia another group with close affinities, though these groups are interconnected through the medium of generalized types occurring in the tropics.

The arguments of Andrews are supported by the long and detailed analysis of palaeobotanical evidence made by Bews [31], who concluded that from the beginning of the Cretaceous period until the end of the Tertiary the vegetation of a large part of the earth enjoyed conditions similar to those of the modern tropical rain forest.

Since Cretaceous times the climate of the world has undergone many changes, the algebraic sum of these changes being loss of heat and moisture. The genial worldwide climate of the Cretaceous has been replaced with the marked division of the present climate into zones. Two of the great divisions of Leguminosae, the Mimosoideae and the Caesalpinioideae, have not adjusted to these changes. With few exceptions they are still confined to the warmer regions of the earth, the tropics and subtropics. The third great division, the Papilionatae, has responded to changed conditions with great vitality. Not only have old tribes such as Sophoreae, Genisteae, and Galegeae adapted themselves so that their species extend from the tropics to the cold regions of the earth, but whole new tribes such as Vicieae and Loteae have arisen entirely within the temperate regions and extended some of their members almost to the frigid limit of plant growth. As an example of this development the tribe Sophoreae appears to have been firmly established in the old world before the separation of Australia from Asia and Africa. The old and decadent nature of the tribe is indicated by the widespread occurrence of very small genera over the tropical world with stunted outliers in the

temperate region. Under the changed climate of the later Tertiary the genus adapted itself in part to colder and less-hospitable surroundings and thus penetrated the temperate regions. But in Australia, and to a smaller extent in Africa, a grand response to altered conditions was made by the development of the specialized offshoot, the Podalyrieae.

> In Australia they are represented by twenty genera and four hundred species, in South Africa by two genera and thirty species. The genus *Pultenaea*, in Australia, with about one hundred species, is a magnificent example of adaptation to environment. Closely allied to it are *Eutaxia*, *Latrobea*, *Phyllota*, *Dillwynia*, and *Aotus*. . . .
>
> As time progressed several of the Australian *Podalyrieae*, such as *Pultenaea* and *Bossiaea* adapted themselves to cold conditions, and a few species established themselves even on the high plateaus of Eastern Australia and Tasmania.
>
> The *Podalyrieae* of South Africa and Australia belong to different subtribes, and they suggest common ancestors in tropical Africa and Asia, from which migrations were made south to lands not connected directly with each other, thus enabling them to develop in different directions. [30].

If one wishes to examine the global distribution of present-day Leguminosae there is only one comprehensive treatise on the Order available, the monograph of Taubert in Engler and Prantl's *Die Natürlichen Pflanzenfamilien* [32]. This monograph is now over sixty years old and very much out of date, particularly as regards numbers of species. Nevertheless it is sufficient on which to base a broad examination of tribal distribution. An analysis of the species enumerated by Taubert is presented in Table 2. In compiling this Table it has been assumed that 'altitude equals latitude'. Thus where species are noted as inhabiting only mountain regions in the tropics, as, for instance, certain species of Trifolium, they have been included under Temperate. Such species are a small minority but if the Table is looked at on a strictly geographic basis they introduce a slight bias in favour of Temperate species. Podalyrieae, which Taubert treated as a separate tribe, have been included in Sophoreae. The tropical genus Abrus, wrongly included by Taubert in Vicieae, has been transferred to Phaseoleae. This genus was correctly placed by Bentham [33] in Phaseoleae where its position was confirmed by the chromosome data of Senn [34]. The evidence advanced later in this paper further confirms this placement.

It is evident from the total figures in Table 2 that the greater number of both genera and species of modern Leguminosae are tropical.

The Sub-order Mimosoideae is entirely tropical and subtropical with the exception of one out of the six tribes, Acacieae. The genus Acacia has, within Australia, invaded the temperate regions and certain species grow even in the alpine regions of south-east Australia and Tasmania.

The Sub-order Caesalpiniodeae is hardly less tropical. In only three out of nine tribes are there species occurring in temperate regions; in Bauhinieae one genus, Cercis, is entirely temperate. In Cassieae also one genus, Ceratonia, is temperate, though a few members of the large genus Cassia extend their subtropical range slightly into temperate regions. In Eucaesalpinieae members of five genera Gleditschia, Gymnocladus, Cercidium, Hoffmanseggia, and Zuccagnia occur in temperate areas.

In the Sub-order Papilionatae the greater number of species are found in temperate regions, but the greater number of genera are tropical. This discrepancy is due to the abundance of small and (according to Andrews) decadent tropical genera and to a comparatively few aggressive and

TABLE 2. *Distribution of Leguminosae*

Tribe	*Genera*	*Species*	*Genera and species in tropics and sub-tropics*	*Genera and species in temperate regions*	*Genera occurring in both tropic and temperate zones*
			MIMOSOIDEAE		
1. Ingeae	10	430	10–430	0	0
2. Acacieae	1	450	1–309	1–141	1
3. Eumimoseae	4	325	4–325	0	0
4. Adenanthereae	9	59	9–59	0	0
5. Piptadenieae	5	56	5–56	0	0
6. Parkieae	2	21	2–21	0	0
Total	31	1,341	31–1,200	1–141	1
			CAESALPINIOIDEAE		
1. Dimorphandreae	4	18	4–18	0	0
2. Cynometreae	11	56	11–56	0	0
3. Amherstieae	28	151	28–151	0	0
4. Bauhinieae	3	158	2–153	1–5	0
5. Cassieae	13	412	12–411	1–1	0
6. Kramerieae	1	13	1–13	0	0
7. Eucaesalpinieae	18	122	14–84	5–38	1
8. Sclerolobieae	10	26	10–26	0	0
9. Tounateeae	7	76	7–76	0	0
Total	95	1,032	89–988	7–44	1
			PAPILIONATAE		
1. Sophoreae (includes Podalyrieae)	59	546	36–142	31–404	8
2. Genisteae	43	968	7–258	39–710	3
3. Trifolieae	6	461	0	6–461	0
4. Loteae	8	144	0	8–144	0
5. Galegeae	64	2,309	34–571	31–738	1
6. Hedysareae	47	716	31–372	16–344	0
7. Dalbergieae	25	327	25–327	0	0
8. Vicieae	5	246	0	5–246	0
9. Phaseoleae	48	797	43–760	5–37	0
Total	305	6,514	176–2,430	141–3,084	12
GRAND TOTAL	431	8,887	296–4,618	149–3,269	14

flourishing temperate genera such as Astragalus which has over 1,200 species. In Papilionatae there is only one tribe, Dalbergieae, that is still wholly tropical. Five tribes, Phaseoleae, Hedysareae, Genisteae, Sophoreae, and Galegeae, show respectively 95, 52, 27, 26, and 25 per cent. of tropical species. Three tribes, Trifolieae, Loteae, and Vicieae are entirely temperate on a climatic basis, and only slightly less so on a geographic basis.

The Significance of Distribution in Relation to Cross-inoculation

Bearing in mind the postulated tropical origin and the present predominantly tropical distribution of the Leguminosae, it is possible to construct a logical picture of the symbiotic pattern in the Order.

We have seen that the Leguminosae arose as a distinct Order in upper Cretaceous times. The symbiosis with Rhizobium so characteristic of the whole Order, even of the most 'primitive' subdivision, the Mimosoideae, must antedate the fission of the Order into its three great branches, and must, therefore, have arisen also in upper Cretaceous or early Tertiary times. The bacteria even at the present day are not obligate symbionts. They spend much of their existence as free-living saprophytic soil inhabitants. As such they possess the ability to survive and multiply in the soil for long periods between the chance sojourns within legume root nodules. They were presumably also thoroughly at home under the soil conditions existing in Cretaceous or early Tertiary times. We have seen that the ancestral legumes arose and thrived under conditions of low land relief, high rainfall and widespread high temperature, i.e. under wet tropical conditions. There is no reason to believe that the chemical and physical factors acting on the soil in those days would be different from the factors in action today. One can reasonably assume that the soil conditions then were similar to those that are found in the wet tropics of the modern world. These are summarized by Richards in his book *Tropical Rain Forest* [35] as follows (p. 205):

> Though varied in many of their properties, the majority of the soils of the rain forest belt share certain important common characteristics. In colour they are bright red or yellow; in texture they are generally loamy or clayey; they are usually deficient in bases, and often in plant nutrients in general; they are almost invariably acid; their humus content tends to be low and is mostly confined to the uppermost horizons; the clay fraction is relatively rich in alumina and poor in silica.

It is a popular misconception that strains of Rhizobium do not thrive under such conditions. Experience of European and American workers is that the bacteria of such species as lucerne, clovers, and peas require a high level of calcium and phosphorus, and when placed in soils low in these elements they do not flourish. This experience tends to be applied also to 'legumes' in a general sense. The work of McCalla [36] has played a large part in fostering this belief. Nevertheless it is a fact that the cowpea type of Rhizobium found in tropical legumes thrives on very low levels of Ca and P under conditions where clover bacteria fail completely. A striking instance of this facility is found in the 'Wallum' soils of coastal subtropical Queensland. These soils show extremely low levels of calcium and phosphorus [37]. However, a wealth of native legumes of such genera as Acacia (Mimosoideae) and Pultenaea, Gompholobium, Daviesia, and Mirbelia (Papilionatae) flourish on them and are well nodulated. Their Rhizobium strains are of the cowpea type [38, and Norris, unpublished]. Turning to truly tropical conditions the remarks of Richards [35] are of very great significance in this connexion. After referring to the prevalence of mycorrhiza in tropical forest trees he makes the following statement (p. 220):

In this connection reference should also be made to the abundance of leguminous trees in many rain forests. Since the soils are so poor in nutrients the possession of root nodules containing nitrogen fixing organisms is probably of considerable advantage to rain-forest plants. In five forest types at Moraballi Creek, British Guiana (p. 236) Davies and Richards [39] found great differences in the proportion of *Leguminosae*. Among trees 4 in. in diameter and over the sample plot figures were as follows:

Forest type	*Mora*	*Morabukea*	*Mixed*	*Greenheart*	*Wallaba*
Percentage of *Leguminosae* (individuals)	59	33	15	14	53

Leguminosae are thus much more abundant in the Mora and Wallaba forest types than elsewhere. Mora community grows on a swamp soil subject to frequent flooding, the Wallaba community on a highly leached podzol; the other forest types are found on red or brown soils of the red earth group, in which nitrification is possibly more active and leaching less intense. There is perhaps some significance in these facts, and in the abundance of *Leguminosae* in rain-forest in general. In rain-forest consociations the single dominant tree species is frequently leguminous.

The ancestral condition of Rhizobium then resembled that of the modern tropical cowpea type in that it was a condition of tolerance for very poor soil nutrient conditions. Furthermore, it is a reasonable assumption that the ancestral condition on the part of the host plant must have been one of cross-inoculation promiscuity. It is a curious fact that the Leguminosae, after evolving the vital symbiosis, failed to evolve a system for ensuring that the appropriate bacterium was automatically transferred with the seed and so was immediately available for the assistance of the new plant. Such transfer with the seed does occur with a few species such as Arachis and Trifolium which bury their seedpods and so automatically inoculate them but these are exceptional in Leguminosae. For the symbiosis to have survived and spread in the early days in the absence of any seed-inoculating mechanism it seems essential that it was a symbiosis with a ubiquitous soil organism and it must have been relatively independent of strain variation within that species of bacterium. The data available on modern species of Leguminosae support this contention. Wilson [3] made a study of the symbiotic promiscuity of the legumes in relation to the degree of open-pollination of the host, and found a very definite association. In general, open-pollinated species will nodulate with large numbers of strains of Rhizobium, and corresponding with the reduction in proportion of open-pollination there is a reduction in the number of bacterial strains successfully used, until closely self-pollinating strains will nodulate with few, one, or none at all. It should be pointed out that this relationship holds only in broad terms. In the author's own work it has been found that *Phaseolus lathyroides* is sufficiently promiscuous to serve as a convenient standard test plant instead of cowpea, yet according to E. M. Hutton (personal communication) it is closely self-fertile. Undoubtedly the converse is also true and there are open-pollinated yet strain-specific species. Nevertheless, when one remembers that there are two partners to the symbiosis each of which may vary

independently, and that there are many factors that may effect nodulation such as nature of root hairs, &c., each of which may also be inherited independently, it would be rather surprising if this were not the case. The general thesis is not altered by such exceptions.

Now open-pollination represents the ancestral condition in the Leguminosae. Stebbins [40] under the heading 'Causes for the degeneration toward self-fertilization', points out that there is little doubt that the genetic system promoting greater flexibility, namely cross-fertilization, is the ancestral one, and that self-fertilized types have evolved repeatedly in various phyla and classes of the plant kingdom, presumably in response to selection pressure in favour of immediate fitness.

One is justified in believing that open-pollination was the primitive condition in the Leguminosae and that the condition of symbiotic promiscuity in certain modern open-pollinated legumes represents the ancestral condition.

Assembling then the following premises:

(*a*) that the bacterial symbiosis arose under wet tropical conditions of low availability of essential soil nutrients;
(*b*) that cross-inoculation promiscuity was the ancestral condition;
(*c*) that the modern cowpea type of Rhizobium is at home in wet tropical conditions of low availability of essential soil nutrients;
(*d*) that a very high degree of symbiotic promiscuity prevails among species having a cowpea type of Rhizobium;
(*e*) that the cowpea type of Rhizobium is common to all tropical species and to a very wide range of species covering each of the great subdivisions of Leguminosae,

it is difficult to avoid the conclusion that the symbiotically promiscuous, culturally slow-growing cowpea type of bacterium as we know it today represents the ancestral type of the organism. It is in fact the type of the genus Rhizobium, and deserves above all the specific designation '*Rhizobium leguminosarum*'. It is more than a little ironical, therefore, to find that in the classification of Rhizobium given in Bergey's *Manual* [41] the cowpea type of Rhizobium alone is not assigned specific rank at all but is noted as a kind of poor relation of *Rhizobium japonicum*, the soybean organism.

The situation may be summed up in the broadest possible way as follows. The ancestral type of Rhizobium was what we know today as the 'cowpea type' and it arose under wet tropical conditions. This ancestral type of Rhizobium has persisted in association with the great bulk of modern Leguminosae, because it is a type which possesses great survival value and because the soil conditions under which it thrives have not altered significantly in humid tropical regions. It is associated with all tribes of Mimosoideae and Caesalpinioideae that have been examined, and with the tribes of Papilionatae still having their affinities in the tropics, namely Dalbergieae, Phaseoleae, Sophoreae, Hedysareae, Genisteae, and Galegeae. In the course of evolution the original wide promiscuity of the host has in many lines been narrowed down, apparently mainly by the loss of genes resulting from an increasing degree of self-

fertilization, so that today there exist many species which, while still nodulating with the ancestral type of bacterium are restricted to one or a few special strains. They have sacrificed the wider survival value of great promiscuity for some more immediate survival value associated with self-pollination or some other factor. The cowpea *Vigna sinensis* would seem to be a species occupying a midway position according to the data of Wilson [3, 4]. The soybean, *Glycine max*, has proceeded much farther along the road and is quite restricted in its symbiotic ability, while on the other hand such a species as *Sesbania macrocarpa* has retained to a high degree the ancestral promiscuity.

The ancestral type of Rhizobium is recognizable by its ability to grow and multiply in soil at a very low level of nutrients, particularly of calcium. None the less it is not restricted to low-fertility soils. There are abundant instances of species requiring the ancestral type of Rhizobium which occur on soils of high fertility and high Ca content. In Australia, for instance, species of such genera as Glycine, Rhyncosia, and Phaseolus occur freely on the fertile black soils of the Darling Downs in Queensland as well as on a range of very poor soils. In the same State areas of fertile high calcium soil are occupied by a dense monospecific stand of Brigalow (*Acacia harpophylla*). The fact that a technique such as that of Leonard [42] in which heavy additions of nutrient, including large quantities of calcium, are made to the rooting medium can be successfully used for the nodulation testing of species requiring cowpea type bacteria, is additional evidence on this point. The ancestral type then may be pictured as one thoroughly at home under poor nutrient conditions but not restricted to such conditions and also quite capable of living under better conditions.

What then is the situation as regards the remaining three tribes of Papilionatae-Loteae, Vicieae, and Trifolieae? Loteae appears to be a young tribe that has evolved in the northern hemisphere, contemporaneously with Vicieae and Trifolieae and with the young southern offshoot of Sophoreae-Podalyrieae [30]. Senn [34] considers that the Loteae, together with the Hedysareae have arisen from primitive 8-chromosome Galegeae, and remarks 'The suggestion that the tribe is a relatively recent one and is still undergoing many evolutionary changes is supported chromosomally by the occurrence of aneuploid numbers 6 and 7 in species closely related to those with the basic number 8, and morphologically by the occurrence of many varietal forms and the difficulty of exact specific and generic differentiation.' From the poor habitats favoured by many of its members, such as dry sandy hill-sides, littorals, and sandy stream borders, and from such cross-inoculation data as are available (e.g. those of Wilson [4]) one would suspect that its symbiotic affinities lie with the ancestral cowpea type of bacterium, but the group as a whole has drastically reduced the degree of its promiscuity during its evolution.

Turning to the tribes Vicieae and Trifolieae we come at last to the special cases that have so confused the issue by being regarded not as special cases but as the norm, both for legumes and for the bacterial symbiosis. Whatever may be the botanical affinity between the two they

are sharply demarcated from the rest of the tribes by their specialized Rhizobium requirements, and by the fact that whole groups of them have developed calcicole habits.

In the tribe Trifolieae there is evidence both from species distribution and chromosome number that the genus Trifolium is an ancient stock. There are groups of Trifolium species inhabiting the mountains in Africa, South America, and California, a distribution suggesting that relics of an ancient population have been left behind. Senn [34] comments that the Trifolieae are remarkable even in the Leguminosae, for constancy of chromosome number, fifty-nine of ninety-six species studied having $n = 8$ and eight others being polyploids of an 8 series. All the species of Melilotus and Parochetus have $n = 8$, but a few species belonging to a 7 series are found in Trigonella, Medicago, and Trifolium. In addition, these five genera of Trifolieae are quite similar morphologically, the generic position of some species being uncertain. It is tempting to speculate that Trifolium represents the ancestral type for the Trifolieae in general, having had its origin in mountain regions in the tropics and from there spread and differentiated principally into northern temperate regions. Bews [31] states (p. 138) that a great many, perhaps the majority of temperate families of plants, have probably arisen first on the mountain ranges of the world from tropical progenitors, the various mountain ranges that began to be built up at the close of the Cretaceous being quite old enough to have seen the origin of much of the modern temperate flora.

A detailed comparison of the Rhizobium relationships of residual mountain groups of Trifolium with the better-known temperate species might be quite rewarding in indicating evolutionary trends. With the limitation of very small quantities of seed for experiment the author has submitted four African species to inoculation *in vitro* by three Rhizobium strains, CB_2 from *Trifolium incarnatum*, CB_3 from *T. repens*, and CB_{45} from *Vigna sinensis*. In Table 3 are shown the number of plants inoculated and the number that nodulated; all nodules were ineffective.

TABLE 3. *Nodulation* in vitro *of African clover species* (*all nodules ineffective*)

Species	*Rhizobium strain used*		
	Crimson clover	*White clover*	*Cowpea*
T. Steudneri . .	2/3	0/3	0/2
T. rueppellianum .	6/11	2/10	0/10
T. semipilosum . .	2/3	1/1	0/3
T. tembense . .	0/4	0/3	0/2

While the results do not suggest that these Trifolium species retain any link with the ancestral cowpea type of Rhizobium, they do indicate that some of them are not closely allied in their Rhizobium requirements to the temperate clover species.

As regards the tribe Vicieae, one cannot do better than quote Senn [34]:

> The true *Vicieae* (*Vicia*, *Lens*, *Lathyrus* and *Pisum*) are a closely related group morphologically and karyologically. They have a common basic chromosome number of $n = 7$, with derived aneuploids of 5 and 6 in *Vicia* and rare polyploids in *Vicia* and *Lathyrus*. This group probably had a common origin in the Mediterranean region where *Lens* and *Pisum* are still endemic. Subsequently *Vicia* and *Lathyrus* have spread over most of the north temperate zone and part of South America, *Lathyrus* having secondary centres of speciation in western United States and the Chile-Argentine region of South America.

These two tribes, the Trifolieae and the Vicieae, have diverged from the main body of Leguminosae, in the author's opinion, because they have exploited the legacy bequeathed to them by their Cretaceous ancestors; the legacy of the huge tracts of calcareous land left by the retreat of the shallow Cretaceous seas. On this land they have thrived and multiplied, and not only have large groups of them developed obligate calcicole habits but so also have their associated symbiotic bacteria. Such development may have reached its peak in species such as lucerne where the link with the ancestral type is now tenuous. The bacterial strains associated with Vicieae and Trifolieae are now obligately dependent on a high level of nutrients in the soil in order to thrive, and at the same time their symbiotic properties have so changed that they are very restricted indeed in the range of species with which they will nodulate.

The differential nutritional requirements of the ancestral type of Rhizobium (represented by a strain from soybean) and the highly evolved calcicole type (represented by a strain from lucerne) are very clearly shown in the data of McCalla [36]—the same data that are sometimes quoted as showing the necessity of a high level of nutrients for the growth of Rhizobium in general. McCalla prepared clays in which the levels of adsorbed calcium and other complementary cations were exactly known, then used these as the basis for aerated liquid media in which the bacteria were grown. His data are summarized in Table 4.

TABLE 4. *Millions of Bacteria per ml. after three Days' Growth in Colloidal Clay Medium (after McCalla)*

Ca *level* m.e./100 gm. *clay*	*Complementary cation*					
	K		Ba		Mg	
	Soya	*Lucerne*	*Soya*	*Lucerne*	*Soya*	*Lucerne*
0	120·0	0·21	65·0	3·6	169·0	64·0
20	190·0	0·35	97·0	4·8	300·0	64·8
40	250·0	120·0	226·8	6·6	450·0	124·2
50	220·0	216·0	145·8	32·4	450·0	135·0
70	240·0	250·0	156·8	43·2	300·0	129·6

It can be seen, for instance, in the Ca-K series that whereas the bacteria from lucerne made no growth at all until more than 20 m.e. of calcium per 100 gm. clay were present, the soybean bacteria achieved a population of 120 millions per ml. in the complete absence of calcium save what

was present in the 0·5 ml. of yeast extract added to the clay, a negligibly small amount.

The author has repeated as nearly as possible McCalla's work for the Ca-K series, using a soybean and a lucerne Rhizobium unrelated to his. A bentonite of 76 per cent. clay content was used to prepare a Ca clay containing 64·5 m.e. Ca/100 gm. clay and a K clay containing 47·4 m.e. K/100 gm. clay. These were mixed in varying proportions to give clay suspensions of increasing Ca content and complementary decreasing K content. After three days' growth the bacterial numbers were estimated by dilution plating with the results shown in Table 5.

TABLE 5. *Millions of Bacteria per ml. after three Days' Growth in Colloidal Clay Medium*

m.e./100 gm. clay		*Soybean Rhizobium* CB_{1336}		*Lucerne Rhizobium* CB_{61}	
Ca	K	*Trial 1*	*Trial 2*	*Trial 1*	*Trial 2*
3·18	47·36	142	159	0	0
15·94	32·76	137	128	97	109
28·71	24·86	140	128	66	63
41·47	16·84	122	109	88	53
54·21	8·94	131	108	77	65
67·0	0·92	102	93	92	105

It is evident that there is a great difference between the two types of Rhizobium in ability to grow at low Ca levels.

Irrespective of minor points of difference it is the author's belief that there are at present two great groups of nodule bacteria associated with legumes, the ancestral low fertility-demanding, tropical, promiscuous, 'cowpea' type, and the recent, symbiotically restricted, temperate, obligate calcicole type. This situation was touched on by Mazé [43] as far back as 1899 when he divided the nodule bacteria into two great groups according to whether their host grew on acid or alkaline soil, though Mazé obviously had no conception of why this might be so, and he certainly did not suspect any connexion with tropical legumes. From the historical point of view and with the support of such data as those of McCalla, it would seem that calcium may be the factor of prime importance in the evolution of this pattern. Possibly the evolutionary drive behind this process is that the high calcium status of both host and bacteria enables a degree of efficiency in the nitrogen-fixation process that is not attainable by the ancestral type of symbiosis. There might, however, be other ecological and nutritional factors. Molybdenum and sulphur may be of great importance. It is now known that an adequate level of molybdenum is vital to the efficient function of the symbiosis in Trifolium and Medicago. What is the molybdenum requirement in the ancestral condition? Molybdenum along with other nutrients is at a very low level in most wet tropical soils and is likely to be unavailable because of acidity. It may be that the ancestral symbiosis required no molybdenum and that this is one extra factor acquired during the evolution of

the calcicole habit. An examination of the molybdenum requirement of some legumes having cowpea type Rhizobium would be of great interest. Data such as those of Vinogradova [44] who examined the molybdenum content of seed of twenty-five species of Leguminosae and found that Caesalpinioideae were in general considerably lower than Papilionatae may be very relevant to this matter.

A Symbiotic Rating as a substitute for the Cross-Inoculation Groups

If the hypothesis that has been advanced is true, it is evident that the present specific designations of Rhizobium are quite untenable, and the cross-inoculation groups are tenable only while they are regarded as exceptions to the general rule in Leguminosae, and not as the typical pattern into which all data must be compressed. They do still have some practical value when applied to such close botanical groups as the Trifolium species.

What is needed, however, is some kind of rating which will reveal quickly for a particular plant species what is the likelihood of encountering difficulty in equipping it with a suitable strain of Rhizobium—in short, a Symbiotic Rating. If sufficient information were available a table of Symbiotic Ratings might be constructed, possibly along the following lines. Let us assume for the moment that all strains of Rhizobium can satisfactorily be divided into two classes, which we shall call Ancestral and Calcicole, by a technique resembling that of McCalla where they are subjected to growth on a medium virtually devoid of calcium. The type of Rhizobium required would then be designated by a capital A for Ancestral or C for Calcicole. This type letter would be followed by letters and figures giving the numbers of genera and species in the three subdivisions of the Leguminosae from which a bacterial strain capable of nodulating the species in question had been obtained. Reciprocal cross-inoculation has no significance whatever in this respect, since we are merely seeking a measure of the degree to which the species has retained the ancestral promiscuity. Thus Cowpea might emerge with a Symbiotic Rating which read:

A:m10–50:c5–15:p25–107.

This would be read to mean that Cowpea requires a bacterial strain of the Ancestral type and that such a strain capable of nodulating it has been obtained from 50 species in 10 genera of Mimosoideae (m), 15 species in 5 genera of Caesalpinioideae (c), and 107 species in 25 genera of Papilionatae (p). Similarly Red Clover, a member of a group that has lost the ancestral promiscuity, might emerge with a Symbiotic Rating which read (based upon the findings of Wilson):

C:m0–0:c0–0:p10–25.

A supplementary note to the Rating could then indicate the genera or species from which a strain of bacteria most likely to nodulate the test species *effectively* could be obtained. The Symbiotic Rating of Cowpea might then finish up as:

A:m10–50:c5–15:p25–107:*Vigna* spp., *Phaseolus* spp., *Glycine* spp.,

and the Symbiotic Rating of Red Clover might emerge as:

C:mo–o:co–o:p10–25:*Trifolium repens*, *T. pratense*.

Such a procedure would take care of even the effectiveness subgroups such as those indicated by Vincent [11] within the clovers and medics.

This suggestion is put forward merely to indicate how a constructive effort to replace the cross-inoculation groups might be made. Before any such attempt could be made much work would be necessary. It must be established by studies similar to those of McCalla whether in fact a satisfactory dividing line can be drawn between ancestral and calcicole types of Rhizobium. The picture should not be confused here by the calcicolic status of the host plant. Since bacterium and host are separate entities their calcium requirement may vary independently. It is entirely possible that a host having a fairly high calcium requirement might be associated with a strain of bacterium having practically no calcium requirement. Nor should the picture be confused by the question of acid tolerance. It is known, for instance, that there are strains of clover bacteria more acid-tolerant than others. This does not mean that they are necessarily doing without Ca since the Ca and H ion are not completely and mutually exclusive in the soil colloid.

Furthermore, we must satisfy ourselves whether there is any sound reason for separating the Medicago type of Rhizobium from the Trifolium type. Superficially there might seem to be so, since there appears to be no serological kinship between the two, and there appear usually to be cultural differences particularly in growth rate. The author prefers to think that the Medicago type merely represents a higher degree of adaptation to the obligate calcicole condition. The type of growth in culture, though it may serve in the very broadest way for grouping strains together, may yet be very misleading. Allen and Allen [24], in discussing the type of growth in culture produced by strains of bacteria from tropical plants that they had placed without doubt in the 'Cowpea cross-inoculation group', noted that:

> In general the physiological and cultural characteristics of the *rhizobia* from the tropical species are in agreement with those previously reported and commonly accepted as normal or typical reactions of 'cowpea' bacteria. . . . The majority of the cultures produced a white or colourless, moist, translucent to opaque type of growth on the agar slants. The cultures isolated from *Samanea saman*, *Andira inermis*, *Albizzia lebbek*, *Piscidia erythrina*, *Parkia africana*, and *Cytisus scoparius*, were exceptions in that the growth was abundant, raised and mucilaginous in almost all instances.

Again, while studying in detail the characteristics of thirty-nine strains of nodule bacteria isolated from species of Sesbania, Johnson and Allen [28] noted that they could be divided into two distinct groups. Those from *S. macrocarpa* and *S. longifolia* were culturally closely similar to the fast-growing bacteria from clover, peas, and beans, while those from *S. grandiflora*, *S. tomentosa*, *S. aculeata*, and *S. sesban*, produced compact opaque colonies, more like those normally recognized as 'cowpea type'. However, in concurrent cross-inoculation studies, all of these

strains produced nodules (admittedly of ineffective type) on *Phaseolus vulgaris* and on *Vigna sinensis*, but on no representative of any other cross-inoculation group.

It is for this reason that the author considers the grouping of the 'bean bacteria' with Burrill and Hansen's [23] Group III which includes Vicia Pisum, Trifolium, &c., to be fortuitous. All tested members of the genus Phaseolus with the exception of four, *P. augustifolius*, *P. coccineus*, *P. multifolius*, and *P. vulgaris*, are placed without hesitation in the 'cowpea group'. These four species are accorded a group of their own, the 'Garden Bean Group', and their bacterium is assigned a specific name, *Rhizobium phaseoli*. The idea of four species within a genus entering into symbiosis with an entirely different species of bacterium appears unnecessarily complicated. It is much more logical to consider this as an example of a small group of species which have drastically reduced their degree of promiscuity and which normally enter into symbiosis with strains of Rhizobium that show an unusual but not unparalleled type of growth in culture. If one looks at the data given by Wilson [4] it is clear that the cross-inoculating affinities of *P. vulgaris* lie very much with species having the 'Cowpea type' of Rhizobium.

The time has come when the course of Rhizobium studies must be reset. By accident of fortune the study of Rhizobium arose and flourished in countries where the legume flora was dominated by species belonging to the tribes Trifolieae and Vicieae, most of which are recent, highly advanced, and not necessarily typical of the Order Leguminosae as a whole. We now possess a great deal of knowledge of the details of the symbiosis in these groups, but that knowledge is shown to be unbalanced. A detailed knowledge of the most highly evolved end link in an evolutionary chain is of limited use if we are quite unable to say whether that knowledge applies to the rest of the chain. If we wish truly to understand the symbiosis we must study it in all its evolutionary stages. We must go back to the most primitive types available and by careful comparative studies arrive at a picture of the symbiotic pattern as a whole. The most pressing need of the student of Rhizobium, curiously enough, is a botanist with the courage to tackle the monumental task of revising Leguminosae as a whole so that we may make a scrutiny of the relative evolutionary status of groups within the Order. A study of the bacteria associated with the most primitive in each of the three great subdivisions would then constitute the base line for a reassessment of Rhizobium. The evolutionary sequence could then be followed by examining the symbiosis of ever more advanced types of legume, until finally we arrive at the tipmost twigs of the legume family tree where work began some 70 years ago.

The prospect of studying the symbiotic relationships of the leguminous tree flora of tropical rain forest is not a particularly attractive one, but it is a task that must be done because it is here that the 'base line' is to be found. Such a study as has been outlined may prove to be quite rewarding as well to the botanist as to the student of Rhizobium. At many a point where taxonomy becomes a matter of personal choice it is possible that comparative studies of the associated Rhizobium might point the

true direction. As indicated earlier, the placement of Abrus with the Phaseoleae rather than the Vicieae by Senn and others on chromosome and morphological data, is further supported by the evidence of Rhizobium, because Abrus possesses true ancestral cowpea type Rhizobium, and the rest of Vicieae possess the Pisum type. Similarly *Trigonella ornithopodiodes* has been transferred to the genus Trifolium as a result of studies made by Nutman (personal communication).

An appreciation of the true position in Rhizobium is of great importance in the development of a country like Australia. This continent was first settled on its temperate southern fringes by people of European stock who introduced European farming methods and European crop and forage legumes, almost all of which have the calcicole type of Rhizobium. Some of these were successful on the large areas of calcium-rich land in southern Australia and on soils enriched with superphosphate. The development of the continent has been broadly speaking a slow pushing northwards into the sub-tropical and finally the truly tropical northern regions. Inevitably these settlers have tried and will continue to try to take with them the temperate leguminous species that they have learned to use and understand. Where calcium-rich land is available this process may be quite successful. The limitations of latitude are more apparent than real; white clover, for instance, grows quite well on the Atherton Tableland in Northern Queensland. The incidence of rainfall, summer instead of winter, is a more serious limiting factor. But, over great areas subject to the heavier tropical rainfall, the very low calcium status of the soils and the associated general poverty in bases introduce a serious complication. On such base-deficient soils the successful growth of lucerne, for instance, will be dependent on making available (and keeping available under a high rate of leaching) an adequate supply of soil calcium. There are vast areas of very poor soil on which the expenditure of money on lime sufficient to produce and maintain effective soil modification is unlikely, even though the quantity necessary per acre for establishment may be reduced to a low level by the techniques of sowing in the drill [45] or pelleting the seed [46]. But apart from the economics of application there exists a considerable risk that application of lime may do more harm than good. Kellogg and Davol [47] discussing present use of Latosol soil types in the Belgian Congo make the pertinent comment:

> Lime is not commonly used, partly because of its scarcity, partly because of uncertain response, and partly because of the great hazard of upsetting the nutrient balance. At these very low levels of bases, a relatively small application of lime, or even of ordinary superphosphate rich in gypsum, may so reduce the intake of magnesium or potassium, or both, as to cause reduction in growth. Then liming such strongly leached, weakly buffered soils, may have serious consequences on several minor nutrients.

For such areas it is unrealistic to think in terms of forcing temperate species such as lucerne and clover into the agricultural and pastoral pattern. In doing so one is trying to put back the evolutionary clock so far as these species are concerned. The greatest emphasis must be on

exploiting the type of legume and the type of Rhizobium that is naturally adapted to such soils without need for their modification, that is, on the tropical legume equipped with the ancestral cowpea type of Rhizobium. There are many herbaceous tropical leguminous species in Australia that have been completely neglected as was pointed out by Davies [48]. For pastoral purposes intensive study of such genera as Desmodium, Indigofera Phaseolus, Psoralea, Glycine, Rhyncosia, Vigna, &c., is clearly indicated. It is encouraging to see that a useful start has been made on this task by Silsbury and Britton [49] in their assessment of the genus Kennedya in Australia.

A determined effort must be made to develop a tropical outlook and to shake off the 'white clover mentality' which in southern Australia, because of the tremendous agricultural significance of Subterranean Clover (*T. subterraneum* L.) treated with superphosphate, might equally be labelled the 'Sub and Super mentality'. This mentality assumes that the spectacular response of clovers and medics to fertilizer obtained in temperate zones is 'normal', and that if tropical species growing on tropical soils do not give equal responses they are not worth working on for pasture purposes. This is far from the truth. The tropical species have adjusted from the earliest beginnings of Leguminosae to a low fertility level, and to expect from them fertilizer responses comparable to their highly specialized calcicole relations is expecting too much. As long as 'White Clover mentality' dominates the thinking of agronomists it will effectively retard the exploitation of low-fertility tropical areas.

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SEASONAL PRODUCTION OF BEEF AND VEAL IN AUSTRALIA AND CONSEQUENT BEEF EXPORTS

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Summary

This paper presents the problem of seasonality of beef and veal production in Australia and its effect on the pattern of exports. The importance of Queensland as a producer of beef and veal for export is clearly shown. The seasonal nature of Queensland production, due mainly to climatic conditions, greatly influences the pattern of Australian exports. Queensland contributed between 71 and 86 per cent. of total beef exports in the years since the 1939/45 war and exported a far greater proportion of its production than the other states.

THE purpose of this paper is to present the problem of the seasonality of beef and veal production in Australia and its impact on the British market.

Although Australia is about thirty times the size of the United Kingdom, production of beef has normally been less than in the United Kingdom. Climatic conditions in Australia are very variable and beef production has been largely relegated to the drier regions by the intense competition for grass by dairy enterprises. Evaporation rates are high and plant growth is restricted, with consequent low stocking rates. Broadly speaking, 50 per cent. of the beef cattle are in Queensland and 25 per cent. in New South Wales. These two states contribute about 70 per cent. of total beef supplies, Queensland's share usually being slightly the larger. Climatic conditions affect production in Queensland more markedly than in New South Wales, where production is less hampered by seasonal droughts and absence of plant growth. These factors of climate promote seasonality of production in Queensland. As nearly all the Australian beef exports to the United Kingdom are from Queensland, United Kingdom imports from Australia have been of a pronounced seasonal pattern. Production in the other states is more evenly distributed throughout the year and is almost exclusively devoted to home consumption.

Australian beef production and exports of beef are given in the Appendix for the years 1935–53. The expansion in output from 458·6 thousand tons to 674·8 thousand tons, for the years ended 30 June 1935 and 1953 respectively, is mainly attributable to the stability and incentives engendered by long-term meat agreements negotiated by the Australian and United Kingdom governments during and after the 1939/45 war. These agreements encouraged capital investment, stock improvement, and increase in herd numbers, in areas which for want of ready markets had been understocked for many years. In the event, the numbers of beef cattle increased from an average of 8·6 million in the five years ended 1939 to 8·7 million by 1944 and to 9·1 million by 1949. At the cattle census on 31 March 1953 there were 10·5 million beef

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cattle. Despite increased production the quantity available for export did not increase up to 1953. This was due to the increasing population in Australia which absorbed a greater proportion of the production despite a decrease in consumption a head.

Australian Production

The total production of beef and veal in Australia is obtained by various methods and in various climatic conditions. There are no available data showing the amounts contributed by the various systems, but a general picture may be obtained by considering production in the individual states. The figures in the Appendix are for carcass beef and veal production on a 'bone-in'-weight basis. The outstanding contribution of New South Wales, Queensland, and to a lesser extent of Victoria, has been a feature of Australian production for very many years. Production in the Northern Territories has been negligible, amounting to no more than 7,000 tons in the last few years. Recent studies by Kelly [1] suggest that the North may have a future as a breeding area, but it appears unlikely that significant changes will occur until capital investment on a large scale is undertaken.

Beef-production data in the Commonwealth Statistician's reports are not in sufficient detail before 1939 for an analysis of seasonal variation for the pre-war period. As seasonality of production is largely determined by climatic conditions in those areas where the variation is greatest, one might infer that the pattern of production before the war was very similar to that which has obtained since 1939.

An analysis [2] of the pattern of production between 1942 and 1947 clearly showed the extremely seasonal character of Queensland production and to a lesser extent that of Western Australia. As, however, the latter state only contributed about 5 per cent. of total production, compared with the 40 per cent. from Queensland, it is the seasonality in Queensland which is of overriding significance. The data published in the above-mentioned analysis are reproduced in Table 1, together with the annual average production in the years 1942–7. As a measure of the seasonal character of production the standard deviation of the monthly indices from the general monthly average of 100 has also been added. About 64 per cent. of the annual production in Queensland was produced in the months May to October inclusive, with peak production occurring in June, July, and August. The evenness of production in New South Wales, Victoria, and Southern Australia was very marked, although their months of largest production coincided with the month of high-level production in Queensland.

In the six years from 1948 to 1953 the Australian annual average production of beef increased to 609,000 tons compared with the annual average of 459,900 tons from 1942 to 1947. The individual states contributed unequally to this increase. New South Wales provided 38 per cent., Victoria and Queensland 24 per cent. each. Thus production from New South Wales provided a larger share of the total output compared with the situation obtaining between 1942 and 1947. From the indices of seasonal variation for the years 1948–53 given in Table 2

(compiled from production data published in the *Quarterly Review of Agricultural Economics*) in comparison with Table 1 it is clear that New South Wales and Victoria increased production and smoothed their seasonal patterns, so that they provided almost level deliveries in each month.

TABLE 1. *Indices of the Average Monthly Production of Beef and Veal in the Individual Australian States 1942–7*

Month	*N.S.W.*	*Vict.*	*Q'land*	*S. Aust.*	*W. Aust.*	*Tasm.*	*Australia* Total*
January	88·3	105·0	52·9	91·9	89·4	103·2	7·0
February	94·0	109·4	62·8	93·4	84·5	100·3	83·8
March	105·3	94·1	89·4	96·7	95·8	95·2	94·8
April	102·6	101·3	87·8	91·1	83·4	100·3	95·5
May	114·0	123·5	121·3	100·3	125·6	108·7	120·1
June	110·4	107·8	135·5	107·6	117·4	103·2	124·1
July	108·9	99·3	140·0	110·2	112·0	100·4	118·1
August	99·4	92·8	146·0	105·6	116·5	100·3	116·8
September	91·4	85·2	123·4	95·8	92·9	95·1	102·2
October	91·6	90·8	100·7	100·8	97·2	97·9	95·7
November	96·9	94·9	77·6	101·3	89·9	98·1	88·3
December	97·2	95·9	62·6	105·3	95·4	97·3	82·6
Average	100	100	100	100	100	100	100
Standard deviation	8·6	9·8	31·3	6·1	13·6	3·6	15·4
Annual average production '000 tons	130·0	88·5	180·3	22·4	22·3	9·3	459·9

* Includes production in Northern Territories and Australian Capital Territory.

TABLE 2. *Indices of the Average Monthly Production of Beef and Veal in the Individual Australian States 1948–53*

Month	*N.S.W.*	*Vict.*	*Q'land*	*S. Aust.*	*W. Aust.*	*Tasm.*	*Australia* Total*
January	95·0	95·7	55·6	99·2	76·2	99·8	80·7
February	98·9	103·2	64·8	92·0	75·0	102·2	86·3
March	99·7	108·6	73·9	86·2	71·6	110·9	90·5
April	97·5	101·1	90·8	98·4	76·7	100·1	95·5
May	105·8	105·1	132·3	99·3	138·9	106·3	116·5
June	102·0	99·6	154·8	110·1	155·3	105·6	122·8
July	102·0	100·6	155·1	106·7	156·3	104·8	122·1
August	101·5	103·0	129·3	115·9	141·6	102·1	115·9
September	101·4	98·2	111·2	97·9	85·1	95·9	102·5
October	96·7	97·4	84·5	106·8	75·6	98·2	92·0
November	102·0	94·8	76·8	93·1	73·7	84·0	89·6
December	97·5	92·7	70·9	94·4	74·0	90·1	85·6
Average	100	100	100	100	100	100	100
Standard deviation	2·9	4·2	33·8	8·3	34·4	7·1	14·7
Annual average production '000 tons	187·0	124·2	217·2	31·3	32·6	12·1	609·0

* Includes production in Northern Territories and Australian Capital Territory.

The increase in output achieved in the other states was accompanied by an increasingly seasonal pattern. Of great significance was the increase in Queensland, where 25 per cent. of the annual output was produced in June and July and 57 per cent. from May to September inclusive. The increases in the other states were comparatively quite small and of less importance to the United Kingdom supplies.

Comparing the situation from 1948 to 1953 with that from 1942 to

1947, it would appear that future increases in output in those states which traditionally supply Australian consumption might be expected to be of a level monthly pattern. The increase in output in Queensland which supplies the United Kingdom was accompanied by an intensification of seasonality. Obviously climatic limitations preclude a wider spread of production over the year. One must infer that unless other states provide a large share of Australian beef exports, the extreme seasonality of Queensland production will continue to influence the seasonal supply of Australian beef for the United Kingdom.

Australian Exports

The data in the Appendix give the total quantity of beef and veal exported from Australia from July 1934 to June 1953. Before the 1939/45 war Australian exports were next in volume to those of Argentina. During and since the war, despite a higher level of production, Australian exports declined and until 1953 a smaller percentage was annually exported as carcass beef than before the war. The increasing Australian population and a tendency to preserve more beef by canning were the causes of the reduced exports of carcass beef. Between 48 and 51 per cent. of Queensland's production from 1935 to 1939 was exported each year. By comparison Victoria exported between 5 and 7 per cent. of its annual production, New South Wales between 3 and 4 per cent., and Western Australia about 30 per cent. Although Western Australia's contribution to exports was normally larger than that of New South Wales or Victoria, its annual production was only about one-sixth and one-quarter of that of New South Wales and Victoria respectively.

Australian total beef exports, those shipped to the United Kingdom and the exports from Queensland, are given in Table 3 for the years 1935 to 1939 and 1945 to 1953. From 1935 to 1939 Queensland contributed annually from 81 to 85 per cent. of Australian exports and the United Kingdom received annually between 87 and 92 per cent. of these. In the post-war period Queensland contributed from 71 to 86 per cent. of the total beef exported and the United Kingdom received between 52 and 87 per cent. of the total exports each year. There has been a tendency in recent years for the United Kingdom share of exports to decline with decreases in the exportable surplus. It would be reasonable to assume that the United Kingdom might expect to receive large quantities, and a large share of the exports, only if the total production were large. Compared with the pre-1939 situation, when about 50 per cent. of production in Queensland was exported, the proportion exported between 1945 and 1953 has varied between 19 and 40 per cent. There has been a tendency for the proportion to decrease in the more recent of these years. Another sign of the pressure of increased population is seen in the proportion of production in New South Wales which was exported between 1946 and 1953. From a level of 6 per cent. in 1946 the exports fell to less than 1 per cent. of production in 1951 and 1952. The increase in production in 1953 allowed exports to rise to 7 per cent. Once again the importance of a high level of production, if exports are to be maintained, must be emphasized.

The pattern of Australian production has been considered above and it has been suggested that the seasonality, which was known to exist in Queensland between 1942 and 1953, already existed before 1939. The course of exports from Australia between 1935 and 1939 (of which

TABLE 3. *Beef and Veal Exports from Australia, 1935–9 and 1945–53*

Year July–June	*Total Australian exports*	*Australian exports to U.K.*	*Exports from Queensland*
	Thousands of tons		
1935/6	87·9	76·4	71·4
1936/7	104·4	95·5	84·8
1937/8	131·2	121·4	107·1
1938/9	121·4	111·2	102·7
1945/6	49·5	18·2	37·6
1946/7	80·5	68·1	57·0
1947/8	105·9	91·7	92·5
1948/9	85·6	67·6	73·0
1949/50	81·4	62·0	70·6
1950/1	70·7	50·6	61·0
1951/2	42·8	22·4	34·2
1952/3	85·9	66·3	64·3

TABLE 4. *Indices of the Average Monthly Exports of Beef and Veal from Australia between 1935–9 and 1945–52*

Month	*1935–9*	*1945–52*
January	45·4	37·1
February	49·2	54·8
March	63·0	61·9
April	90·1	36·5
May	126·0	72·6
June	199·0	122·6
July	152·2	164·7
August	130·7	181·6
September	103·9	183·5
October	80·6	117·6
November	86·4	108·5
December	73·5	58·6
Average	100	100
Standard deviation	42·3	52·1
Annual average exports '000 tons	111·2	73·8

Queensland contributed more than 80 per cent.) supports the contention. Data given in Table 4 show the indices of seasonal variation of exports between 1935 and 1939 and between 1945 and 1952.

Before 1939 the peak month for exports was June, whereas between 1945 and 1952 August and September were the months of largest

exports. More than 50 per cent. of the exports occurred between May and August before the war, whereas in latter years 64 per cent. of the exports were shipped between June and November. The seasonality of exports has been similar in the two periods, but there has been a tendency for seasonality to become more marked. This is indicated by the greater standard deviation from the mean of 100 in 1945–52. The smaller exports in the latter period, due to the pressure of population in those states which produced beef with little seasonal variation probably accounted for the higher seasonal index between 1945 and 1952.

An analysis of indices of seasonal variation of exports from the main exporting states between 1947 and 1953 in quarterly periods shows that

TABLE 5. *Indices of the Average Quarterly Exports of Beef and Veal from Australia between 1947–53*

Period	*N.S.W.*	*Victoria*	*Queensland*	*W. Australia*
1st quarter . . .	114·8	89·7	47·7	8·5
2nd ,, . . .	83·5	122·5	89·0	12·2
3rd ,, . . .	112·8	85·3	178·6	203·2
4th ,, . . .	88·9	102·5	84·7	176·1
Average . . .	100	100	100	100
Standard deviation . .	13·9	14·4	48·1	90·2
Annual average exports '000 tons . . .	5·0	2·3	65·4	6·2

New South Wales and Victoria have had reasonably level deliveries for exports. Their patterns of exports have been complementary in that New South Wales had slight export peaks in the first and third quarters of the year, while Victoria's peaks occurred in the second and fourth quarters. The large concentration of exports from both Queensland and Western Australia has occurred in the third quarter. The indices are set out in Table 5, together with the standard deviations.

It is clear that so long as beef exports depend so much on Queensland and Western Australian supplies, a high degree of seasonality will continue. The recent increases in production in the Southern states and the consequent increase in exportable surpluses has tended to make exports slightly less seasonal.

However, large quantities have left Australia between June and September with peak shipments in August and September. Thus large deliveries of Australian beef arrived in the United Kingdom in the autumn at a time when United Kingdom slaughtering is seasonally above the average for the year. During the war imported frozen beef was retained in cold store for periods varying from a few days to several months, depending on the supply situation. Such beef was cold-stored for longer periods than had been common before the war. Long-period storage is expensive and any measures which reduce an unnecessary cost are to be welcomed by both producers and consumers.

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APPENDIX

Australian Beef and Veal Production and Exports, 1935–53

Year ended 30 June	*Production Thousands of tons*							*Exports*	
	N.S.W.	*Vict.*	*Q'land*	*S. Aust.*	*W. Aust.*	*Tasm.*	*Aust.* Total*	*Exports '000 tons*	*% of production*
1935	153·4	94·3	155·6	21·9	23·8	8·1	458·6	92·1	20·1
1936	167·4	113·9	149·9	23·9	26·0	8·3	490·2	87·9	17·1
1937	179·4	127·6	179·5	27·6	25·7	9·8	551·3	104·4	18·9
1938	191·8	126·7	211·5	25·9	29·8	9·9	596·8	131·2	22·0
1939	172·0	114·0	207·0	24·7	27·7	10·9	559·2	121·4	21·7
1940	173·0	103·7	195·5	23·6	26·5	10·6	535·0	127·3	23·8
1941	139·4	99·5	190·5	23·6	25·9	10·7	492·9	88·7	18·0
1942	159·2	112·3	199·5	23·1	24·8	11·3	533·5	52·3	9·8
1943	156·0	105·3	200·4	28·1	22·4	11·4	534·5	10·1	1·9
1944	145·2	100·5	187·3	26·2	19·9	11·0	500·7	21·2	4·2
1945	125·9	99·3	175·3	23·0	18·2	9·2	461·1	28·0	6·1
1946	134·4	75·4	137·3	21·1	23·6	8·3	406·6	49·5	12·2
1947	139·9	95·6	190·2	24·4	26·3	8·2	487·8	80·5	16·5
1948	161·9	105·1	226·5	27·2	29·5	8·1	562·0	105·9	18·8
1949	180·3	118·0	202·5	29·6	32·8	9·8	577·3	85·6	14·8
1950	185·6	124·6	211·5	32·6	35·4	12·3	606·5	81·4	13·4
1951	192·8	136·6	232·4	36·4	34·0	14·1	651·5	70·7	10·9
1952	184·3	137·2	177·6	31·1	32·2	14·4	581·9	42·8	7·4
1953	217·3	123·6	252·5	31·1	31·8	13·8	674·8	85·9	12·7

* Australian total production includes a small quantity produced in Northern Territories and Australian Capital Territory.

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THE HAZARDS OF PARASITIC GASTRO-ENTERITIS IN SHEEP RUNNING UNDER CONDITIONS OF INTENSIVE STOCKING

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Summary

A field experiment carried out over three successive seasons demonstrated that there is considerable danger from parasitic gastritis under conditions of intensive sheep grazing. It is clear that weather and management are important factors deciding whether disease breaks out or not. It is concluded that no set rules can be made on the desirable level of sheep-stocking but that every sheep-owner must himself experiment to decide the rate of stocking which under his own conditions give maximum production with minimum hazard from parasitic disease.

THE rate of sheep-stocking in Great Britain varies from as little as one ewe to 3 or 4 acres on the poorest land to as many as ten or even more ewes to the acre on rich sheep pasture. On the majority of sheep farms, however, the rate of stocking is about two ewes to the acre, but in recent years interest has been stimulated in the possibility of increasing this level, with a consequent increase in agricultural productivity. Observation has shown that certain sheep-farmers have adjusted their systems of flock management to enable them to carry considerably more stock to the acre than their neighbours, and it would be worth while to ascertain to what extent their methods could be applied by other sheep-farmers. The introduction of improved strains of grasses together with new methods of grassland management also lead one to believe that heavier stocking than at present might be possible in the future. Any increase in the rate of stocking of grassland predisposes to a higher incidence of parasitic disease, especially parasitic gastro-enteritis, and an assessment of this hazard would provide valuable data for the stock-raiser in planning a grazing system. Accordingly, when it was learnt that trials, in which sheep were to be grazed intensively, were to be carried out at the Experimental Husbandry Farm at Winchester, the opportunity was taken to study the risk of parasitism to which the sheep were exposed.

Materials and Methods

The pasture used in the experiment, which began in 1953, had been reseeded in 1952 with the following seeds mixture:

3 lb. Italian Ryegrass 2 lb. S. 23 ,, 8 lb. S. 24 ,, 4 lb. S. 143 Cocksfoot 9 lb. S. 37 ,, 4 lb. S. 48 Timothy 1 lb. S. 184 Wild White Clover	26 lb. per acre.

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Twenty acres of this pasture were divided into five 4-acre plots and grazed by 100 ewes and their lambs. The experiment continued over three grazing seasons, during the first of which the flock consisted of a mixture of Cluns and Half-breds, but during the other two seasons only Cluns were used. The plots were grazed rotationally at 6–10-day intervals, according to the rate of growth of the grass, and when this was too great cattle preceded the sheep to bring the grass down to sheep level. Supplementary feed was given from time to time when necessary. The flock of sheep which was ordinarily kept on the farm and grazed extensively was used as a control for comparison with the intensively grazed flock.

Routine anthelmintic treatment was given to both intensively grazed and control flocks at approximately monthly intervals, phenothiazine being used except on one occasion when copper sulphate–nicotine sulphate mixture was used.

The helminthological observations carried out during the course of the investigation were pasture larval counts on the experimental plots together with faecal egg counts on samples of both the experimental and the control flocks. Also a post-mortem examination was made on any animal which died during the course of the experiment. The amount of work involved precluded the collection of weekly herbage samples from each plot, and it was decided to collect herbage from each plot just before the sheep entered in the course of the rotation; in this way a measure was obtained of the level of infestation to which the sheep were exposed when they entered each plot. The herbage samples were collected and examined by the method described by Taylor [1]. The faecal samples, which were collected each month from a random sample of twenty ewes and twenty lambs from each group, were examined by either the McMaster method or a modified Clayton-Lane flotation method as appropriate.

Course of the Experiment

The investigation began in April 1953 and the plots were grazed rotationally until the latter part of August, when the poor rate of growth of the grass necessitated the removal of the flock on to corn stubble. The herbage on the plots recuperated and sheep were returned there on 4 December 1953. They grazed the plots until 1 February 1954 when snow and inclement weather necessitated removal of the flock to more accessible fields for hand feeding. Beginning 20 April 1954, ewes were drafted back on to the plots when their lambs were born, and rotational grazing was practised throughout the summer. The lambs were weaned and removed from the plots on 12 August 1954, but the ewes remained there until 7 September, when they were removed to another part of the farm for tupping. The flock returned to the plots on 20 October, and rotational grazing was carried on until 10 December, when the sheep were again removed and the plots rested until 21 April 1955. The ewes, with their lambs, then returned to the plots and rotational grazing was practised until the experiment terminated on 10 August 1955.

Results

The detailed results of the helminthological observations are given in the Appendix. Tables 1 (*a*), 1 (*b*), and 1 (*c*) refer to the 1953 grazing season; Tables 2 (*a*), 2 (*b*), 2 (*c*), and 2 (*d*) to the 1954 grazing season; and Tables 3 (*a*), 3 (*b*), and 3 (*c*) to the 1955 grazing season. The egg count

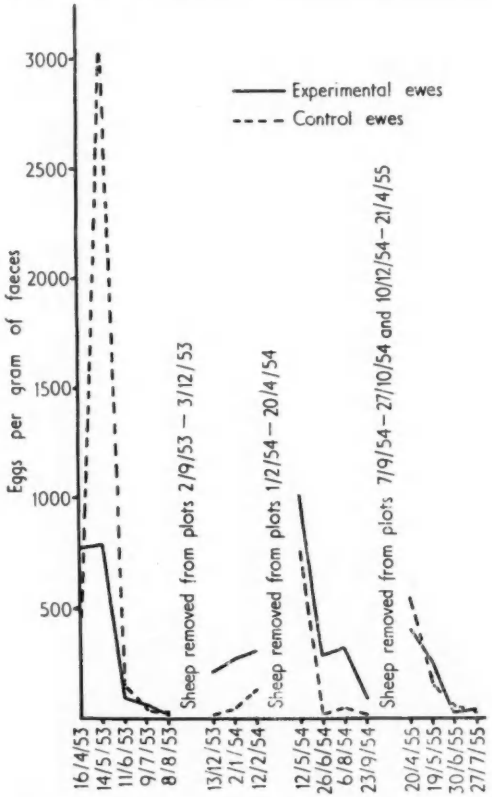

FIG. 1. The ewes of both flocks during the period of observation.

Note.—1. Egg count data were not available for the period 27/10/54–10/12/54.
2. At the points marked 20/4/55, 19/5/55, 30/6/55, and 27/7/55 the examinations of the control flock were actually carried out on 22/4/55, 24/5/55, 28/6/55, and 25/7/55.

data have been summarized in Figs. 1 and 2. Fig. 1 shows the changes in mean monthly egg count for the two flocks of ewes over the whole experimental period. In Fig. 2 the mean monthly egg counts of both the experimental and control lamb flocks are plotted on the same scale as that used in Fig. 1. In addition the main findings are summarized below.

1953 grazing season.—Although the experimental ewes had high egg counts initially, anthelmintic treatment reduced them to a low level and kept them low. The control ewes showed much the same picture. At the beginning of the experiment the lambs in the experimental group were a little over a week old and had developed only light infestations when the first treatment with phenothiazine was given in May. During

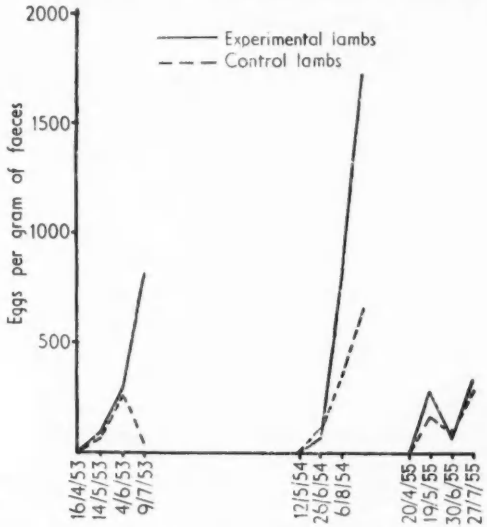

FIG. 2. Fluctuations in the mean monthly faecal egg count of the three crops of lambs produced during the period of observation.

Note.—1. The same scale is used as in Fig. 1 for easy comparison.
2. At the points marked 20/4/55, 19/5/55, 30/6/55, and 27/7/55 the examinations of the control flock were actually carried out on 22/4/55, 24/5/55, 28/6/55, and 27/7/55.

the summer their faecal egg counts increased and in spite of treatment given in June some had high counts at weaning time. The third treatment, given at weaning, would doubtless be beneficial in reducing the worm burden of the lambs, but they were sold before faecal egg counts could be carried out. The control lambs showed an entirely different picture and were carrying only light infestations at weaning time. The pasture larval counts increased to a peak at the beginning of July but a fall took place during August, although the count was still appreciable when the sheep made their last circuit of the plots. The figures show that the sheep must have been consuming large numbers of infective larvae during the summer and it seems certain that fatal infestations would have developed had anthelmintic treatment been omitted.

1954 season.—No appreciable loss of larvae from the pasture herbage occurred between the end of the 1953 grazing season and December 1953, when the sheep returned to the plots, and during the initial grazing period until February 1954 the level of pasture larval infestation

remained almost static. A spectacular drop occurred in the period when inclement weather necessitated removal of the sheep from the plots, and even when sheep returned to the plots the count remained low until June, when a sudden increase occurred. The count remained high during the rest of the summer; the wet weather which persisted at that time no doubt favoured larval development and was responsible for the high counts recorded.

Anthelmintic treatment kept the egg counts of the experimental ewes low, but in spite of this treatment the experimental lambs developed quite high faecal egg counts and a severe outbreak of parasitic gastritis occurred, resulting in the death of a number of lambs. An outbreak of parasitic gastro-enteritis also occurred in the extensively grazed control flock, but it was not so severe as that which occurred in the experimental flock. Two factors without doubt contributed greatly to the causation of disease in the experimental flock. First, the dose of phenothiazine employed was inadequate to give full control of the worms. The dose was that recommended by the manufacturer of the drug (20 gm. for adult sheep), and this has been shown to be only partially effective in control of parasitic gastritis [2]. The second factor was a change in the order of plot rotation at the beginning of June, which brought the sheep on to highly dangerous ground which had been grazed only 2 weeks previously.

1955 season.—In this third year of the trial more favourable results were obtained. Although the egg counts of the experimental ewes were fairly high in April, regular monthly treatment with phenothiazine brought them down to a low level again, and during June, July, and August pasture contamination by the ewes must have been slight. The lambs' faecal egg counts were also kept low by treatment. A very similar picture was seen in the control sheep which were subjected to the same routine of anthelmintic treatment. Pasture larval counts on the experimental plots reflected the lower rate of pasture contamination which obtained this season. The counts were low throughout most of the season, and whereas during 1954 counts of over 1,000 larvae per pound were the rule, during 1955 such counts occurred on two occasions only and during this season most of the counts were below 200 larvae per pound.

Discussion

Three years of intensive grazing of sheep at the rate of five ewes to the acre has demonstrated that parasitic gastro-enteritis may become a serious hazard under these conditions. This is not surprising since overstocking of pastures has long been recognized as an important factor in the causation of parasitic gastro-enteritis. It had been thought possible, however, that the shortness of the herbage on which rotational intensive grazing was practised might result in the desiccation and death of many of the larvae on the pasture herbage, with a consequent reduction in the apparent danger of this system of grazing. Experience over the 3 years of the experiment shows that the weather had a considerable influence on the incidence of parasitic gastro-enteritis. During the first

two seasons of the experiment, wet weather during the summer favoured larval development and high pasture larval counts were recorded. In the drier third season low pasture larval counts were observed. The weather does, therefore, appear to influence the number of infective larvae found on the pasture herbage and may make all the difference between success and failure under conditions of intensive grazing where the hazard of parasitic gastro-enteritis is high.

The danger of parasitic gastro-enteritis under conditions of intensive grazing have been recognized by other workers. Ross and Graham [3] in a series of trials carried out in New South Wales and Tasmania recognized that heavy stocking of improved pastures involved a risk of this disease even when rotational grazing was practised, but they considered that the risk was compensated by the improved condition of the animals compared with those running on unimproved natural pastures. Nevertheless, they recorded better production of wool and mutton by sheep receiving anthelmintic treatment than by those left untreated. Ross [4], summarizing the position at that time, stated: 'It is necessary to appreciate the fact that whether parasitism becomes of greater or less importance on such [improved] pastures is largely a question of balance between the adequacy and degree of improvement of pastures on one hand and the intensity and duration of stocking practised, together with the predisposition to heavy parasitism owing to seasonal conditions or special topographical features on the other.'

Morgan [5], using adult goats in a trial of heavy stocking lasting a year, showed that in the summer improved nutrition and other factors tended to diminish the risk of parasitic infestation resulting from overstocking. In his experience, however, in the winter the dangers of parasitic disease increased in spite of extra feeding with hay and concentrates. Ross, Chamberlain, and Turner [6], in a trial in which weaners run on two different rotation systems were compared with similar sheep continuously grazed on the same area, reported better production and a lower degree of parasitism in the rotated groups compared with the continuously grazed group. These sheep were, however, much more resistant to parasitism than the lambs used in previous experiments.

Gordon and Turner [7], investigating the parasitic burden in groups of sheep run on two different systems of rotation and a group continuously grazed, also concluded that rotational grazing did not favour the development and persistence of infestation with *Haemonchus contortus* and *Trichostrongylus* spp. The sheep carried only light worm burdens and were beyond the age when they would act as sensitive indicators of variations in host-parasite relationships related to management and nutrition. The dangers of parasitism on weaners and adult sheep are therefore much less than in lambs under conditions of intensive stocking and rotational grazing, although Morgan's work indicates that even these may be affected.

Although much of the work quoted above, and the results of the present investigation, indicate parasitic gastro-enteritis to be a severe limiting factor deterring production under intensive grazing, certain farmers have been able successfully to adjust their system of husbandry to enable

them to carry much heavier sheep stocks than current practice would indicate as possible. Local conditions will play a part in deciding to what extent the level of stocking may be raised, and the weather will be an important factor. From the present work the routine use of anthelmintics seems to be essential, but no hard-and-fast rules can be laid down. It is for every farmer to experiment under his own conditions to determine the maximum stocking-level permissible under his conditions, consistent with maximum production per acre and minimum risk of parasitic disease.

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See Appendix on following pages.

APPENDIX

TABLE 1 (*a*). *Egg Counts of Experimental Sheep during the 1953 Grazing Season*

No.	*16.4.53*	*14.5.53*	*11.6.53*	*9.7.53*	*8.8.53*
Experimental ewes					
C. 1	..	2,700	100	50	49
2	..	..	1	1	14
3	500	1,000	300	7	33
4	1,000	1,000	100	..	..
5	1,000	..	100	50	..
6	..	500	100	15	0
7	26	200	100	..	8
8	900	400	0	2	0
9	..	..	400	200	2
10	1,100	2,200	200	100	..
11	1,600	1,100	100	3	2
12	100	1,300	3	11	..
13	..	1	..	3	13
14	200	800	..	300	3
15	1,800	..	..	0	..
16	..	600	0	50	..
17	..	200	5	50	7
18	..	300	8	..	..
19	..	100	..	24	..
20	300	200	0	..	0
Experimental lambs					
101	0	..	..	..	..
102	0	..	..	..	..
103	0	57	546	4,600	..
104	0	26	..	..	..
105	0	400	..	..	..
106	0	100	63	206	..
107	0	86	363	3,500	..
108	0	100	755	..	..
109	0	..	..	..	..
110	0	300	338	..	..
111	0	0	223	400	..
112	0	6	193	350	..
113	0	30	522	300	..
114	0	..	200	300	..
115	0	1	100	24	..
116	0	24	400	..	..
117	0	1	100	100	..
118	..	0	100	33	..
119	0	100	200	150	..
120	0	..	..	..	..
121	0	..	..	..	..
122	..	..	200	..	..
123	..	..	500	200	..
124	..	..	3	1,500	..
125	..	..	2	150	..
126	..	..	900	450	..

All sheep except Clun lambs dosed with phenothiazine 27.5.53

All sheep dosed with phenothiazine 24.6.53

All lambs dosed with phenothiazine at weaning and all ewes on 8.8.53

TABLE 1 (*b*). *Egg Counts of the Control Sheep during the 1953 Grazing Season*

No.	*16.4.53*	*14.5.53*	*11.6.53*	*9.7.53*	*8.8.53*
Control ewes					
F. 1	100	300	..	100	38
2	500	..	400	..	..
3	..	400	100	7	7
4	300	800	100	100	2
5	..	35,200*	..	..	..
10	400	900	33	14	13
11	500	..	..	..	..
19	100	..	100	100	100
26	100	2,000	100	..	..
42	100	200	200	5	60
48	300	1,300	100	..	0
56	600	1,300	400	4	..
57	1,600	1,100	200	100	..
58	1,700	..	..	..	..
72	300	800	108	53	..
89	22	200	100	..	1
92	46	100	200	14	0
101	400	1,400	..	2	29
110	1,000	1,300	18	7	1
114	100	900	100	16	0
Control lambs					
3	0	400	..	..	..
4	0	100	600	20	..
5	..	56	..	..	..
11	0	100	..	..	..
20	0	100	..	5	..
22	0	16	..	..	..
23	..	200	500	..	..
29	0	300	700	..	..
30	0	13	..	..	..
36	..	6	300	..	..
37	..	8	300	7	..
43	0	10	..	150	..
45	..	3	25	50	..
49	..	2	14	50	..
61	..	7	200	50	..
62	..	1	100	27	..
64	..	0	100	100	..
70	..	2	..	49	..
73	..	11	..	..	..
82	..	1	20	8	..

Ewes dosed with phenothiazine 27.5.53

Ewes and lambs dosed with phenothiazine 24.6.53

* Died 26.5.53.

TABLE 1 (*c*). *Pasture Larval Counts and Grazing Record of the Experimental Plots during the 1953 Grazing Season*

Plot no.	*Date of sample*	*No. of larvae per pound of herbage*	*Sheep in plot*	*Cattle in plot*	*Remarks*
3	16.4.53	0	16.4.53–24.4.53		
4	23.4.53	25	23.4.53–2.5.53		
5	1.5.53	29	2.5.53–11.5.53	20 cattle 24.4.53–2.5.53	
1	11.5.53	0	11.5.53–19.5.53	21 cattle 2.5.53–8.5.53	
2	19.5.53	43	19.5.53–23.5.53	22 cattle 8.5.53–15.5.53	
3	22.5.53	3	23.5.53–29.5.53	20 cattle 21.5.53–26.5.53	Phenothiazine administered 27.5.53
4	30.5.53	7	1.6.53–6.6.53	20 cattle 26.5.53–29.5.53	
5	6.6.53	63	6.6.53–12.6.53	20 cattle 29.5.53–1.6.53	
1	12.6.53	92	12.6.53–19.6.53		
2	19.6.53	127	19.6.53–25.6.53	.. ..	Phenothiazine administered 24.6.53
3	25.6.53	299	25.6.53–1.7.53		
4	1.7.53	1,113	1.7.53–7.7.53		
5	7.7.53	2,811	7.7.53–15.7.53		
1	14.7.53	762	15.7.53–22.7.53		
2	22.7.53	801	22.7.53–27.7.53		
3	27.7.53	136	27.7.53–4.8.53		
4	4.8.53	643	4.8.53–10.8.53	.. ..	Phenothiazine administered 8.8.53
5	10.8.53	567	10.8.53–17.8.53		
1	17.8.53	356	17.8.53–23.8.53		
2	22.8.53	429	23.8.53–27.8.53		
3	27.8.53	383	27.8.53–2.9.53		
4	2.9.53	403			

TABLE 2 (*a*). *Egg Counts of Experimental Sheep during the 1954 Grazing Season*

Number	*3.12.53*	*2.1.54*	*12.2.54*	*12.5.54*	*26.6.54*	*6.8.54*	*23.9.54*
Experimental ewes							
581	500	700	300	1,000	1,200	300	16
582	49	100	300	700	79	L.T.100	16
583	400	200	700	..	600	200	32
584	300	400	400	..	200	200	1
585	200	500	700	..	..	..	..
586	100	300	100	900	200	100	2
587	300	100	100	2,400	200	500	..
588	500	400	400	..	..	..	..
589	200	100	100	..	18	100	8
590	81	300	100	..	62	L.T.100	30
591	200	..	800	700	100	1,000	..
592	300	700	500	1,200	200	100	..
593	34	100	100	800	3	200	..
594	400	500	200	..	400	400	800
595	17	35	500	..	..	..	..
596	49	100	200	..	..	..	..
597	18	6	100	800	33	L.T.100	0
598	100	100	100	..	..	..	..
599	200	100	200	400	..	100	..
600	200	300	100	1,200	500	..	2
560	..	..	..	..	..	..	9
561	..	..	..	..	9	600	5
562	..	..	..	..	500	0	0
563	..	..	..	..	500	300	0
Experimental lambs							
110	..	..	..	5	190	..	700
111	..	..	..	..	26	400	..
112	..	..	..	0	74	..	2,600
113	..	..	..	4	95	200	400
136	..	..	..	0	122	800	3,600
147	..	..	..	0	22	800	2,500
163	..	..	..	0	19	800	900
171	..	..	..	0	48	100	..
180	..	..	..	..	17	600	3,100
182	..	..	..	..	100	400	1,300
183	..	..	..	0	166	300	1,500
189	..	..	..	..	52	300	1,300
190	..	..	..	..	92	1,200	1,200
191	..	..	..	0	119	4,600	..
192	..	..	..	0	21	200	700
193	..	..	..	..	..	300	..
198	..	..	..	..	9	..	..
199	..	..	..	..	37	500	700
200	..	..	..	0	9	500	3,700

Dosed with phenothiazine 9.6.54 — Dosed with Cunic 15.7.54 — Dosed with Phenothiazine 10.8.54

TABLE 2 (*b*). *Egg Counts of Control Sheep during the 1954 Grazing Season*

Number	*3.12.53*	*2.1.54*	*12.2.54*	*12.5.54*	*26.6.54*	*9.8.54*	*23.9.54*
Control ewes							
F. 1	41	38	19	..	..	..	..
3(478)	69	39	..	..	..	..	..
8	30	129	73	..	26	200	44
10	1	4	..	..	2	1	0
42	0	6	..	100	2	..	..
48	8	39	..	700	25	0	..
56	1	0	..	500	15	0	0
57	..	39	35	400	10	100	9
71	..	2	1	200	3	0	0
75	3	57	138	..	..	100	12
85	1	1	2	200	0	..	0
89	0	1	11	..	8	0	..
92	0	24	102	500	6	0	..
101	0	8	35	300	2	0	67
106	0	0	..	..	..	..	..
110	0	9	..	..	4	0	0
114	0	..	..	..	5	0	13
517	..	..	..	..	..	..	..
456	8	69	50	200	..	..	17
461	..	31	400	..	19	100	3
467	..	121	600	5,000	..	..	..
478	..	..	..	200	8	100	1
15	..	..	..	..	56	..	1
120	..	..	..	..	4	1	2
Control lambs							
DL. 60	..	..	..	0	96	3,900	700
61	..	..	..	2	113	8	300
62	..	..	..	0	290	75	1,500
63	..	..	..	0	6	200	1,200
64	..	..	..	..	151	100	1,200
65	..	..	..	0	259	24	200
66	..	..	..	..	431	300	800
67	..	..	..	0	95	100	400
68	..	..	..	..	..	300	200
69	..	..	..	..	..	200	1,100
70	..	..	..	0	126	300	800
71	..	..	..	..	85	27	300
72	..	..	..	0	8	300	500
73	..	..	..	1	7	37	94
74	..	..	..	..	109	100	900
75	..	..	..	..	105	500	700
76	..	..	..	..	47	300	500
77	..	..	..	..	13	100	400
78	..	..	..	..	15	100	600

Dosed with phenothiazine 14.6.54 — Dosed with cunic or phenothiazine 16.7.54 — Dosed with phenothiazine 9.8.54

TABLE 2 (*c*). *Pasture Larval Counts and Grazing Record of the Experimental Plots during the 1954 Grazing Season*

Plot no.	*Date of sample*	*No of larvae per pound of herbage*	*Sheep in plot*	*Cattle in plot*	*Remarks*
4	4.12.53	200	4.12.53–11.12.53		
5	11.12.53	482	11.12.53–19.12.53		
1	18.12.53	152	19.12.53–24.12.53		
2	No collection		24.12.53–29.12.53		
3	29.12.53	123	29.12.53–4.1.54		
4	4.1.54	212	4.1.54–11.1.54		
5	11.1.54	452	11.1.54–19.1.54		
1	19.1.54	395	19.1.54–1.2.54		
			Sheep absent from plots 1.2.54–20.4.54		
4	20.4.54	48	20.4.54–28.4.54		
3	24.4.54	11	28.4.54–4.5.54	26 cattle 21.4.54–29.4.54	
2	4.5.54	3	4.5.54–12.5.54	32 ,, 27.9.54–4.5.54	
1	12.5.54	12	12.5.54–19.5.54		
5	20.5.54	24	19.5.54–24.5.54	32 ,, 15.5.54–19.5.54	
4	No collection		24.5.54–31.5.54		
3	31.5.54	11	31.5.54–8.6.54		
1	8.6.54	697	8.6.54–11.6.54	.. ..	Phenothiazine administered 9.6.54
			Sheep removed for shearing 11.6.54–16.6.54		
1	No collection		16.6.54–23.6.54	30 ,, 13.6.54–16.6.54	
2	23.6.54	501	23.6.54–28.6.54	26 ,, 4.6.54–13.6.54 31 ,, 16.6.54–23.6.54	
4	28.6.54	5,148	28.6.54–5.7.54	28 ,, 2.6.54–4.6.54	
5	5.7.54	718	5.7.54–9.7.54	31 ,, 23.6.54–28.6.54	Copper sulphate-nicotine sulphate mixture administered 5.7.54
3	9.7.54	1,620	9.7.54–17.7.54		
1	17.7.54	2,575	17.7.54–26.7.54		
5	No collection		26.7.54–30.7.54		
2	30.7.54	93	30.7.54–5.8.54		
4	5.8.54	1,048	5.8.54–19.8.54	.. ..	Phenothiazine administered 10.8.54
3	19.8.54	1,713	19.8.54–25.8.54	27 ,, 7.8.54–13.8.54	
1	25.8.54	684	25.8.54–7.9.54	27 ,, 13.8.54–19.8.54 27 ,, 24.8.54–25.8.54	
			Sheep removed prior to tupping 7.9.54		

Cattle also grazed each plot for a time after the sheep were removed for tupping. Cattle were finally removed on 24.10.54.

TABLE 2 (*d*). *Showing Results of Post-mortem Examinations on Sheep Dying during the course of the 1954 Grazing Season*

Date received	Number	Abomasum					Small intestine								Remarks
		Total	Ostertagia circumcincta	Ostertagia trifurcata	Trichostrongylus axei	Immature nematodes	Unidentified nematodes	Total	Trichostrongylus vitrinus	Trichostrongylus colubriformis	Ostertagia circumcincta	Cooperia	Nematodirus filicollis	Strongyloides	Immature nematodes	Unidentified nematodes	
10.8.54	DL. 123	100	..	..	..	..	100	12,700	7,796	2,124	..	3,079	..	..	..	..	Experimental group
10.8.54	CR. 545	1,400	800	500	..	100	..	4,200	200	400	200	..	3,400	..	..	..	Control
10.8.54	DL. 193	37,800	30,200	3,800	..	3,800	..	10,300	3,700	3,500	300	1,808	500	200	300	..	Experimental group
23.8.54	DL. 134	37,800	32,130	5,670	..	..	..	24,100	11,086	7,230	2,410	..	..	..	..	2,892	Experimental group
25.8.54	DL. 300	16,200	13,284	1,944	324	648	..	27,400	9,316	2,836	548	7,672	2,740	..	3,288	..	Experimental group
11.9.54	DL. 204	4,300	4,100	..	..	200	..	2,200	100	..	100	500	..	..	..	1,500	Experimental group

TABLE 3 (*a*). *Faecal Egg Counts of Experimental Sheep during the 1955 Grazing Season*

Number	*20.4.55*	*19.5.55*	*30.6.55*	*27.7.55*
Experimental ewes				
DL. 81	900	300	..	3
82	1,000	900	19	100
83	500	200	0	26
84	600	100	3	1
85	200	200	17	8
86	300	..	..	0
87	300	..	2	40
88	200	100	4	100
89	400	500	200	..
90	1,200	700	100	76
CD. 427	35	11	0	18
461	100	200	7	2
509	300	..	..	..
563	400	200	4	0
567	200	200	4	14
568	400	100	1	..
571	300	300	4	100
574	200	25	0	1
577	100	100	0	..
582	400	100	3	16
Experimental lambs				
DL. 390	2	40	9	136
407	2	241	4	1,000
411	1	100	200	1,400
423	0	400	200	200
424	1	98	77	0
425	6	300	26	200
428	0	..	..	200
447	0	300	..	600
451	0	..	11	..
455	0	200	..	200
466	0	200	8	200
470	0	500	105	600
475	0	1,100	3	500
479	0	500	..	100
480	1	100	3	10
483	0	500	9	200
484	0	100	7	200
492	0	50	300	200
502	0	50	23	4

Dosed with phenothiazine 20.4.55 | Dosed with phenothiazine 20.5.55 | Dosed with phenothiazine 29.6.55 | Dosed with phenothiazine 28.7.55

TABLE 3 (*b*). *Faecal Egg Counts of Control Sheep during the 1955 Grazing Season*

Number	*22.4.55*	*24.5.55*	*28.6.55*	*25.7.55*
Control ewes				
F. 7	300	..	2	7
9	400	100	..	..
15	200	53	12	50
18	600	12	1	0
21	200	100	20	0
23	84	33	..	3
27	1,200	500	20	3
28	1,500	200	7	58
30	100	28	..	1
38	600	100	137	200
40	700	100	..	26
52	800	600	..	6
53	700	200	107	31
55	500	300	20	3
65	200	100	..	4
70	300	7	..	5
76	1,800	100	101	..
96	100	27	2	..
97	100	200	167	3
Control lambs				
DL. 306	2	100	19	49
313	0	300	100	200
314	4	200	100	85
315	11	100	200	800
321	0	100	12	100
327	0	100	70	41
330	0	100	106	55
331	0	100	..	400
333	2	300	11	300
334	0	100	3	74
336	0	..	2	..
337	0	100	100	400
338	0	100	..	500
347	19	200	100	..
348	5	100	24	400
349	14	300	100	150
357	0	84	21	300
443	0	43	500	800
471	0	200	200	..
571	0	500	..	200

Dosed with phenothiazine 22.4.55

Dosed with phenothiazine 23.4.55

Dosed with phenothiazine 28.6.55

Dosed with phenothiazine 25.7.55

TABLE 3 (*c*). *Showing Grazing Record and Herbage Larval Counts of Experimental Plots during the 1955 Grazing Season*

Plot	*Date of sample*	*Larvae per pound*	*Sheep in plot*	*Cattle in plot*	*Phenothiazine treatment*
3	28.10.54	130	28.10.54–5.11.54		
2	5.11.54	36	5.11.54–13.11.54		
1	13.11.54	194	13.11.54–19.11.54		
5	19.11.54	37	19.11.54–24.11.54		
4	24.11.54	66	24.11.54–1.12.54		
3	1.12.54	53	1.12.54–7.12.54		
2	7.12.54	68	7.12.54–10.12.54		
1	10.12.54	32			
			Sheep absent from plots 10.12.54–21.4.55		
1	21.4.55	15	21.4.55–27.4.55	.. ..	20.4.55
2	27.4.55	3	27.4.55–4.5.55		
3	4.5.55	131	4.5.55–10.5.55		
4	10.5.55	41	10.5.55–17.5.55	32 cattle 6.5.55–10.5.55	
5	17.5.55	29	17.5.55–24.5.55	32 ,, 10.5.55–17.5.55	
1	24.5.55	1,107	24.5.55–31.5.55	32 ,, 17.5.55–24.5.55	30.5.55
2	31.5.55	450	31.5.55–9.6.55	28 ,, 24.5.55–26.5.55	
3	9.6.55	328	9.6.55–16.6.55	29 ,, 7.6.55–9.6.55	
4	16.6.55	825	16.6.55–23.6.55	29 ,, 9.6.55–16.6.55	
5	23.6.55	4,517	23.6.55–30.6.55	29 ,, 16.6.55–23.6.55	29.6.55
1	30.6.55	257	30.6.55–7.7.55	29 ,, 23.6.55–30.6.55	
2	7.7.55	458	7.7.55–11.7.55	29 ,, 30.6.55–7.7.55	
3	11.7.55	123	11.7.55–19.7.55		
4	19.7.55	493	19.7.55–27.7.55		
5	27.7.55	34	27.7.55–3.8.55		
1	3.8.55	26	3.8.55–9.8.55		

THE VALUE OF ROCK PHOSPHATES FOR DIRECT APPLICATION

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Summary

In field experiments Gafsa, Curacao, and Morocco rock phosphates were more effective than Florida pebble phosphate. For swedes and turnips Gafsa phosphate was nearly equivalent to superphosphate on soils with pH values below 6·5; for potatoes and for grassland Gafsa phosphate was only one-third as effective as superphosphate, even on acid soils. In both pot and field experiments rock phosphates were almost useless on neutral and alkaline soils.

A number of different crops were grown in a pot experiment. Morocco phosphate was equivalent to superphosphate for radish; for swedes, rape, and buckwheat it was about half as effective. For mustard, clover, ryegrass, timothy, wheat, barley, rye, and lettuce Morocco phosphate was of little use.

Rock phosphates from a number of countries were tested in pot experiments on radish. Materials from Morocco, Algeria, Java, Egypt, and Curaçao were a little less effective than that from Gafsa. Nauru Island phosphate was much less effective than Gafsa phosphate. Florida pebble phosphate, phosphatic chalk from Taplow (Berks.), and phosphates from Nigeria, Christmas Island, Kola (U.S.S.R.), Uganda, and Rhodesia were of very little use when applied to radishes grown in acid soils.

Field and pot experiments failed to provide any consistent evidence that rock phosphates should be ground more finely than is customary (80 to 90 per cent. passing the 100-mesh B.S. sieve).

Rock phosphates acted more slowly than superphosphate in pot experiments on radishes; their efficiencies tended to increase as the experiments were continued. The solubilities of rock phosphates were not appreciably increased by 'composting' under acid conditions with wheat chaff in laboratory and pot experiments.

ALTHOUGH the greater part of the rock phosphate mined is chemically processed to make soluble phosphate fertilizers, an appreciable quantity is applied directly to the soil after being ground finely. Page [1] reports that 550,000 tons of P_2O_5 were used in this way in 1955. In early experiments in the United Kingdom Scott Robertson [2] showed that ground rock phosphates could be useful fertilizers for grassland and that on acid soils and in areas of high rainfall they may be as effective as basic slag; soft rock phosphates from North Africa gave higher yields than harder materials such as pebble phosphate from Florida. In later experiments Crowther [3] showed that Gafsa phosphate from Tunis was as effective as high-soluble basic slag for grass grown on acid soils. The results of more recent field work have been published by Crowther, Warren, and Cooke [4] and by Cooke [5]. The purpose of this paper is to discuss the factors affecting the agricultural values of rock phosphates, with special reference to recent work, much of which has not been published.

The value of any rock phosphate used for direct application depends

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on the source of the material, its physical characteristics, the nature of the soil, and the crop which is grown. These factors were often investigated simultaneously in pot and field experiments but, for clarity, they are discussed separately here.

Comparisons of different kinds of rock phosphate

Field experiments carried out since 1940 tested a restricted number of rock phosphates, but a wider range of materials was tested in pot experiments. Analytical data for the phosphates used in the work summarized here are stated in Table 1. (Different batches of some rock phosphates were used in different experiments; for these materials the stated analyses are averages for the various batches.)

TABLE 1. *Analyses of Rock Phosphates used in Field and Pot Experiments*

Place of origin	*Total* P_2O_5 %	*Per cent. solubility of* P_2O_5 *in citric acid* [6]	*Fluorine* %
Cheribon, Java	29·7	43	0·2
Christmas Island	38·3	30	1·1
Curaçao	34·0	24	0·4
England (Taplow phosphatic chalk)	13·9	2	1·2
Egypt: Safaga	28·7	39	4·0
Safi	30·8	35	3·5
Nauru Island	35·6	26	2·5
Nigeria	23·6	3	0·9
North Africa: Algeria (Constantine)	24·8	..	..
Morocco	32·5	34	3·3
Tunis (Gafsa)	27·8	40	3·4
Rhodesia	31·3	..	..
Uganda (Tororo)	25·6	16	2·0
U.S.A. (Florida pebble phosphate)	33·5	18	3·7
U.S.S.R. (Kola concentrate)	40·3	9	3·0
Steamed bone flour	34·2	78	..

Field experiments.—In the United Kingdom supplies of North African phosphates were cut off early in the 1939–45 war and alternative materials were imported from Florida (U.S.A.) and the Netherlands West Indian island of Curaçao (which supplied a hard rock, relatively free from fluorine). Later in the war Morocco phosphate was again imported. These three kinds of phosphate were compared in field experiments on swedes and on grass. The results have been summarized previously by Cooke [5].

Swedes. Florida rock phosphate was tested in 1941 and gave yields similar to those given by only one-quarter as much phosphorus applied as superphosphate (in experiments on reseeded grass it was also very inefficient and was not considered to be worth further testing). In the same experiments the phosphorus in Gafsa and Curaçao phosphates was about half as effective as that in superphosphate.

In later field experiments in 1943–6 both Morocco and Gafsa phos-

phates were equivalent to only two-thirds as much phosphorus supplied as superphosphate, in experiments on soils with pH values below 5·5. In a much larger series of field experiments carried out in 1951–3 Gafsa phosphate was practically equivalent to superphosphate on soils having pH values below 6·5.

Grassland. Field experiments carried out from 1941–6, largely on very acid soils in Wales, compared ground rock phosphates with standard materials (either high-soluble basic slags or superphosphate) for direct reseeding of grass. The effects of the fertilizers were estimated by visual scoring for the degree of establishment of sown species of grasses and clovers. Gafsa, Morocco, and Curaçao phosphates behaved similarly and gave establishment as satisfactory as amounts of standard materials supplying from one-quarter to one-half as much phosphorus. Observations in later years suggested that Gafsa and Curaçao phosphates may give as good growth of grass as the more soluble materials.

Potatoes. In field experiments in 1951–3 Gafsa phosphate was equivalent to only one-third as much phosphorus supplied as superphosphate on soils with pH values below 6·5. It was useless on soils with higher pH values.

Pot experiments.—The war-time field experiments on swedes and grass were supplemented by many pot experiments, mostly using radishes as the test crop, which compared several kinds of rock phosphates on soils having various pH values. The technique used in small-scale pot experiments has been described by Crowther *et al.* [7]. Generally each pot contained 250 g. of crushed flint and 50 g. of soil. Basal dressings of nitrogen, potassium, sodium, and magnesium were given. Six to eight radish seeds were sown in each pot and the seedlings were thinned to three plants per pot. The crops matured in five to six weeks in good growing conditions; frequently second and third crops were taken after adding further N and K fertilizers but no more phosphate.

The results of the pot experiments are presented here in summary form. Where the crops were analysed to determine phosphorus uptake, the percentages of the added fertilizer-phosphorus taken up have been stated. Where only yield data were available the results were used to calculate percentage equivalents of the tested materials in terms of a standard fertilizer. Thus in most experiments the superphosphate response curve was drawn and from this curve the amounts of P_2O_5 applied as superphosphate which would have been needed to give the same yields as the dressings of rock phosphate used were read off. These quantities were expressed as percentages of the amounts of P_2O_5 actually applied (as rock phosphate) to give 'percentage superphosphate equivalents'. This method is approximate but it is a drastic test of alternative phosphates; it is not appropriate where the tested materials give higher yields than the standard fertilizer or where the response curve for the standard is flat.

A pot experiment on radishes carried out in 1941 compared several rock phosphates using Rothamsted clay-loam soils having different pH values. The percentages of added phosphorus taken up by the crop are stated in Table 2. Florida phosphate was of little use even on very acid

soil, Gafsa and Curaçao phosphates were more active on the two acid soils; on alkaline soil neither had any effect.

TABLE 2. *Percentage of Added Phosphorus taken up by Radishes in an Experiment using Small Pots (No. 7)*

Soil pH	*4·6*	*5·9*	*6·4*	*7·5*
	Percentage uptake of added phosphorus			
Superphosphate	48	42	47	41
Basic slag	47	50	45	34
Gafsa	17	15	9	0
Curaçao	12	12	4	0
Florida	0	4	1	0

An additional experiment on turnips was carried out in glazed earthenware pots each containing 20 lb. of a mixture of 80 per cent. soil and 20 per cent. sand. An acid soil (pH 5·7) and an alkaline soil (pH 7·8) were used; both were Rothamsted clay-loams. Curaçao and Gafsa phosphates were tested together with a phosphatic chalk from Taplow (Berks.) containing 13 per cent. P_2O_5. The results are summarized in Table 3. In the acid soil turnips recovered about three-quarters as much phosphorus from Gafsa phosphate as from superphosphate, Curaçao was only about half as effective as Gafsa phosphate, Taplow phosphate was practically useless. On the alkaline soil all three mineral phosphates had little effect.

TABLE 3. *Percentage Recovery of Added Phosphorus by Turnips Grown in an Experiment using Large Pots*

	Acid soil (pH 5·7)	*Alkaline soil (pH 7·8)*
	Percentage uptake of added phosphorus	
Superphosphate	22	13
Basic slag	19	9
Gafsa	16	2
Curaçao	9	4
Taplow	2	1

The experiments summarized in Tables 2 and 3 afford an interesting contrast. For radishes, with a short growing season, Gafsa and Curaçao rock phosphates were less effective, relative to superphosphate, than for turnips which need approximately twice as long to mature.

In Pot Experiment No. 7 on radishes rock phosphates from Taplow (Berks.), Nauru Island, and Nigeria were tested; the crops grown were not analysed to determine phosphorus uptakes and the yields with these materials were therefore excluded from Table 2. They were used to determine the percentage superphosphate equivalents listed in Table 4, after averaging the results of the first and second crops on all four acid

soils. Rock phosphates from Florida and Nigeria and the phosphatic chalk from Taplow were all of very little value; Nauru phosphate was a little better than these materials and Gafsa and Curaçao phosphates were much more effective.

TABLE 4. *Results of Pot Experiment No. 7 on Radishes (the yields of two crops grown on four acid soils were averaged)*

	Percentage superphosphate equivalents
Basic slag	112
Superphosphate	100
Gafsa	28
Curaçao	14
Florida (mineral phosphates)	2
Taplow	1
Nauru	6
Nigeria	3

Another pot experiment (No. 8) on radishes tested normal (between 0·200 mm. and 0·100 mm.) and fine (smaller than 0·063 mm.) fractions of several rock phosphates. Three acid soils were used, having pH values of 4·4, 5·4, and 6·0. The yields were used to derive percentage superphosphate equivalents by graphical interpolation, after averaging data for the three soils (Table 5).

TABLE 5. *Results of Pot Experiment No. 8 on Radishes Testing Rock Phosphates (averaging yields on three acid soils)*

	Normal grinding	*Fine grinding*	*Mean*
	Percentage superphosphate equivalents		
Rock phosphate from			
Gafsa	29	37	33
Curaçao	29	28	28
Cheribon	25	24	24
Morocco	21	24	23
Egypt (Safaga)	24	23	23
Nauru	11	16	13
Christmas Island	6	7	6
Florida	5	4	4
Kola	1	0	0
Steamed bone flour	41	48	44

Steamed bone flour was also tested in this experiment. It is like rock phosphate in having an apatite structure but its physical properties are likely to make it of maximum value for crops; it was half as effective as superphosphate. Gafsa was the most effective rock phosphate, being one-third as good as superphosphate. Curaçao and Cheribon phosphates (which contain little fluorine) were a little less effective than Gafsa phosphate, as was Morocco phosphate. Nauru and Christmas Island phosphates were much less effective than superphosphate; Florida and Kola phosphates were almost inert.

A further pot experiment (No. 15) on radishes compared three African rock phosphates. The well-known material from Gafsa (Tunis) was compared with Constantine (Algerian) phosphate and with a rock phosphate from Tororo (Uganda). Steamed bone flour was also included. Three crops of radish were grown. On alkaline soil none of the rock phosphates had any appreciable effect, even for the later crops. The results of the experiment are summarized in Table 6 by stating percentage superphosphate equivalents of the rock phosphates after averaging results on three acid soils.

TABLE 6. *Results of Pot Experiment No. 15 on Radishes Testing Rock Phosphates. (The results on three acid soils are averaged)*

	Crop 1	*Crops 1+2*	*Crops 1+2+3*
	Percentage superphosphate equivalents		
Rock phosphate from			
Gafsa, Tunis	28	38	61
Constantine, Algeria	15	27	53
Tororo, Uganda	0	0	2
Steamed bone flour	56	76	100

Uganda phosphate was quite useless; Constantine phosphate was a little inferior to Gafsa phosphate but both materials were better for later crops and, on average of the three crops, they were more than half as efficient as superphosphate. The efficiency of steamed bone flour improved in a similar manner and on the basis of the sum of three crops it was as effective as superphosphate.

In a later pot experiment (No. 18) on radishes coarse and fine Gafsa and Morocco rock phosphates, together with phosphates from Rhodesia and Uganda, were tested using an acid soil. The results are summarized in Table 7 by stating for the first crop, and for the sum of the first and second crops, percentage superphosphate equivalents of the tested phosphates. (The superphosphate response curve for the second crop was too flat to allow accurate interpolation.)

TABLE 7. *Results of Pot Experiment No. 18 on Radishes Testing Rock Phosphates*

	Crop 1	*Crops 1+2*
	Percentage superphosphate equivalents	
Gafsa phosphate		
Coarse	29	72
Normal fineness	38	100
Morocco phosphate		
Coarse	38	69
Normal fineness	23	49
Rhodesian phosphate	0	0
Uganda phosphate	4	7

Rhodesian phosphate was quite useless and the material from Uganda was only slightly active. Gafsa and Morocco phosphates were both active, being approximately one-third as efficient as superphosphate for the first crop and much more effective on the sum of two crops. Differences between coarse and fine materials are discussed later.

Pot Experiment No. 72 on radishes tested Gafsa and Morocco phosphates together with coarse and normal grindings of Safi (Egyptian) phosphate. The percentages of added phosphate recovered are summarized in Table 8, after averaging the results on three acid soils. The mineral phosphates were much more effective for the second than for the first crop. Of the materials tested Gafsa was best, Morocco was next best, and Safi phosphate was inferior to the other rock phosphates.

TABLE 8. *Results of Pot Experiment No. 72 on Radishes Testing Three Kinds of Rock Phosphate (averaging the results obtained on three acid soils)*

	Crop 1	*Crop 2*	*Crops 1+2*
	Percentage of added phosphate recovered		
From			
Superphosphate	52	6	58
Gafsa (mineral phosphates)	19	27	46
Morocco (mineral phosphates)	14	20	34
Safi (coarse) (mineral phosphates)	12	13	25
Safi (normal) (mineral phosphates)	9	15	24

Fineness of Grinding of Rock Phosphates

All discussions in this paper on the fertilizer value of rock phosphate, apart from those in this section, refer to *normal* materials ground as is customary so that 80 or 90 per cent. passes the 100-mesh B.S. sieve (having apertures of 0·152 mm.).

Field experiments.—Wartime field experiments (described by Crowther *et al.* [4]) tested *coarse* (about 60 per cent. through 100-mesh sieve) and *normal* (about 80 per cent. through 100-mesh sieve) grindings of Curaçao, Gafsa, and Morocco phosphates. In swede experiments coarse and normal batches of Curaçao phosphate gave similar yields. For establishing reseeded grass, there was no gain from the finer grinding of Gafsa phosphate, but coarse grindings of Morocco phosphate were inferior to normal batches.

Very few field experiments had been carried out in the United Kingdom to test rock phosphates ground more finely than normal until a series was initiated in 1954 to compare two grades of Gafsa phosphate:

Normal: 90 per cent. through 100-mesh sieve (0·152 mm.).
Fine: 90 per cent. through 300-mesh sieve (0·053 mm.).

There were only small differences between yields of grass, swedes, and kale given by these normal and fine grades of Gafsa phosphate. For grass the normal material and for swedes the fine material was a little better, for kale the two grades were equal.

Pot experiments.—In Pot Experiment No. 8 on radishes (Table 5)

there were no major differences between yields given by normal and fine grades of the rock phosphates tested; the finer grades of Gafsa, Morocco, and Nauru phosphates supplied slightly more phosphorus to the crops than the normal grades. In Pot Experiment No. 18 on radishes (Table 7) coarse Gafsa phosphate was inferior to normal material for both the first and second crops. In contrast a normal grinding of Morocco phosphate gave lower yields than coarser materials. Pot Experiment No. 72 on radishes (Table 8) showed that there was no gain from normal as compared with coarse grinding of Safi phosphate.

Neither the field experiments nor the pot experiments provide any consistent evidence that rock phosphate should be ground more finely than is customary (80 to 90 per cent. passing the 100-mesh B.S. sieve). This conclusion is important since fine grinding is expensive and difficult, particularly with the harder rock phosphates such as that from Curaçao. The main virtue of mineral phosphates is their cheapness relative to chemically processed phosphates like superphosphate. Any extra preparation which adds materially to their cost, without a corresponding increase in efficiency, is likely to hinder the direct use of rock phosphates on the soils and crops to which they are suited.

The Immediate Value of Rock Phosphate for Various Crops

Field experiments.—Field experiments on rock phosphate have been used to provide an approximate quantitative valuation of Gafsa rock phosphate (ground to normal fineness) for swedes, potatoes, and grass; average 'percentage superphosphate equivalents' of Gafsa phosphate are stated in Table 9. Gafsa rock phosphate is a very useful fertilizer for

TABLE 9. *Approximate Percentage Superphosphate Equivalents of Gafsa Rock Phosphate used for Various Crops*

Crop	*Very acid soils (pH to 5·5)*	*Acid soils (pH 5·5 to 6·5)*	*Neutral soils (pH over 6·5)*
Swedes and turnips	80	72	12
Potatoes	34	37	4
Grassland			
for establishment	*c.* 34		..
for hay production	*c.* 30		..

swedes and turnips grown on acid and very acid soils; for potatoes it is much less useful and likely to be quite unsuitable in areas of moderate or low rainfall. For establishing grass Gafsa phosphate was only one-third as effective as the same amount of phosphorus applied as superphosphate or high-quality basic slag. Early experiments described by Scott Robertson [2] and by Crowther [3] placed a higher value on rock phosphate relative to basic slag for grassland. In Scott Robertson's experiments the tested fertilizers supplied 200 lb. of P_2O_5 per acre. In experiments described by Crowther, phosphate fertilizers were applied at 100 lb. P_2O_5 per acre, but the shape of the response curve was not determined. The lower efficiency of rock phosphate demonstrated by

the recent experiments may be due to the use of lower rates of application, which make the comparisons more sensitive, and because the experiments were only continued for one season; both circumstances favour the more quick-acting materials such as superphosphate or high-quality basic slags.

Pot experiment.—An experiment carried out in 1944 in small pots compared the responses of twelve different crops to several phosphate fertilizers. A mixture of clay-loam soil (pH 6·3) with crushed flint was used. Yields from two successive sowings of each crop were combined to estimate (by graphical interpolation) the amounts of monocalcium phosphate needed to give the same yields as 100 parts of the other phosphates. These quantities, being percentages of the amounts of tested phosphate actually applied, provide the 'percentage monocalcium phosphate equivalents' stated in Table 10.

In this slightly acid soil the ability of crops to use phosphorus derived from mineral phosphate varied greatly. For radishes Morocco phosphate gave yields similar to those given by monocalcium phosphate and basic slag; for swedes, rape, and buckwheat, Morocco phosphate was active, but inferior to the other phosphates. Mustard, clover, grasses, cereals, and lettuce made practically no use of Morocco phosphate.

TABLE 10. *Comparisons of Morocco Phosphate, Basic Slag, and Monocalcium Phosphate for Various Crops*

Crop	*Bessemer basic slag*	*Morocco rock phosphate*
	Percentage monocalcium phosphate equivalents	
Swedes	80	50
Rape	70	65
Mustard	105	15
Radish	125	120
Clover	90	20
Ryegrass	55	20
Timothy	75	0
Wheat	100	10
Barley	100	15
Rye	85	5
Buckwheat	85	45
Lettuce	70	0

It has been known for many years that certain crops are able to make full use of rock phosphates while others make little use of them even on acid soils. An explanation of this phenomenon has never been provided. Gross differences in the patterns of root growth must determine the number of points of contact between roots and areas of soil enriched with decomposing apatite. Crops with well-developed fibrous roots are

best equipped to utilize phosphates distributed irregularly over the internal surfaces of soil. It is also possible that crops which take up considerable quantities of calcium, or which have roots with marked affinities for calcium, promote the decomposition of insoluble calcium phosphates.

The Rates and Methods of Action of Rock Phosphates

Immediate effects.—Pot experiments described above show that rock phosphates tended to be markedly inferior to superphosphate for a first crop of radishes (harvested approximately 6 weeks after sowing) but that for later crops in the same experiments rock phosphates were more effective. Rate of action of Curaçao phosphate was investigated in more detail in Pot Experiment No. 41. Radishes were grown in acid soil of pH 5·4; parts of the crop were harvested at intervals of 15, 20, 25, 30, and 40 days after sowing. The results are summarized in Table 11.

TABLE 11. *Rate of Uptake of Phosphorus from Superphosphate and Rock Phosphate by Radishes (Pot Experiment No. 41)*

	P_2O_5 *taken up per pot from 18 mg.* P_2O_5 *added* — *days after sowing*				
	15	*20*	*25*	*30*	*40*
Superphosphate	2·3	5·2	9·2	11·2	12·4
Curaçao rock phosphate	0·5	1·3	3·0	6·3	9·3
No phosphate added	0·1	..	1·2	..	3·8
	Relative uptake, taking superphosphate as standard				
Superphosphate	100	100	100	100	100
Curaçao rock phosphate	22	25	33	56	75
No phosphate added	4	..	13	..	31

Fifteen days after sowing the radishes had taken up only about one-fifth as much phosphorus from Curaçao phosphate as from superphosphate. Uptake from Curaçao phosphate increased steadily until at the end of the experiment this material had provided three-quarters as much phosphorus as was provided by superphosphate. The soil phosphorus was also utilized by the radishes to an increasing extent and 40 days after sowing, it had provided one-third as much phosphorus as was provided by the dose of superphosphate applied.

Residual effects.—Considerations of the rates of action of rock phosphates lead naturally to discussions on their residual effects over long periods. Very few United Kingdom field experiments testing rock phosphates on arable crops have been continued for more than one year. The residual effects of phosphate applied a year previously have generally been found to be small and difficult to measure, probably because the dressings were diluted with soil by ploughing and cultivating for the second crop. Phosphate given to permanent grass is not diluted with soil by cultivation and may have more lasting effects than on arable land. In field experiments on grass described by Crowther [3] soluble phos-

phates were superior to rock phosphate in the first year but in the second and third years both kinds of fertilizer behaved similarly. On established grassland water-soluble phosphates are dissolved by rain and penetrate rapidly to the roots. Rock phosphates can be utilized only after they have decomposed and penetrated into the soil; such fertilizers cannot be expected to be as effective as soluble materials unless the experiments are continued for more than one season.

Phosphate fertilizers are used for two quite different purposes and it is important in these discussions not to confuse them. When manuring is intended for the *immediate* benefit of the crop a quick-acting phosphate is needed to stimulate root growth; water-soluble materials are then likely to have special merits. When phosphate manuring is intended to *maintain* soil phosphate reserves, or to provide for a slowly-growing established crop, water-soluble materials are not essential and rock phosphates could be used on appropriate soils.

Although the 2 per cent. citric-acid test [6] used for basic slags has often been used for valuing rock phosphate, there is no agreed empirical test for distinguishing these materials. At present it seems more useful to know the type and origin of a particular batch of phosphate rock than to determine its solubility in a particular extracting solution.

Composting with rock phosphates.—It has been suggested [8] that the availability of rock phosphate may be increased by composting with organic materials. Increases in solubility of the phosphorus may be caused by the acidity developed or by complexing of calcium ions by organic anions present in the compost. Experiments were carried out by H. L. Nixon and the author to examine the effect of acid 'composting' on the solubility of rock phosphates. Wheat-straw chaff was incubated with and without rock phosphates at 30° C. for 1 month; the pH values fell to 4·6. At the end of the incubation, the amounts of water-soluble phosphorus in the composts were measured. Comparisons were made with similar mixtures of chaff and rock phosphates which had not been incubated. Of the total phosphorus added as rock phosphate, the following amounts had been rendered water-soluble by the composting process:

From	*Per cent. of added phosphorus rendered soluble*
Gafsa rock phosphates	7
Curaçao rock phosphates	8
Florida rock phosphates	3

In further work similar 'composts' of wheat chaff incubated with rock phosphate were tested in a pot experiment on radishes. Three crops were grown. The amounts of phosphorus recovered by the radish from all three kinds of rock phosphate were much smaller than the amounts recovered from equivalent superphosphate. 'Composted' rock phosphate were not superior to untreated materials. This work suggests that the acidity developed during decomposition of organic matter will not markedly increase the solubility of rock phosphate.

The decomposition of fluorapatite.—In spite of a great deal of laboratory

work in many countries, the reactions involved in the decomposition of fluorapatite (the principal constituent of many rock phosphates) remain obscure. It is, however, clear that when fluorapatite has dissolved the phosphate ions formed will behave in the same way as phosphate ions derived from any other phosphate fertilizer. They may be used by plants, or they may diffuse away from the apatite crystal and react with other constituents of the soil. There is no reason to believe that 'soil phosphate' derived from rock phosphate is in any way different from 'soil phosphate' derived from superphosphate.

Where rock phosphates are used, not for their immediate effects but to maintain a satisfactory soil-phosphate status, it is important that the apatite should decompose completely within a reasonable time. If the decomposition of fluorapatite crystals is not sufficiently quick, or if the decomposition is promoted only by certain crops or soil conditions, rock phosphates are not likely to be generally useful. Further laboratory work is needed to investigate the factors which affect the solution of apatites in soils. Field work is also needed to define more closely the crops and soils for which rock phosphates are economic fertilizers and also to measure their rates of action and 'residual' effects.

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EFFECT OF CROSSING TWO BREEDS OF EGYPTIAN SHEEP ON WOOL CHARACTERISTICS

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Summary

The purpose of the experiment was to study the wool characteristics of Ossimi and Rahmani sheep, and of the F_1 hybrids from these two breeds. A crossbreeding experiment has been conducted for three years, comprising 65 pure Ossimi, 58 pure Rahmani, 44 crossbred sheep produced from Ossimi rams × Rahmani ewes and 62 from the reciprocal cross. Observations were taken at 6, 11, 17, and 23 months old.

The results showed that both breeds of sheep belong to the long-wool type. The wool of the crossbred animals was intermediate in staple length and fibre length between the two parent breeds at all ages studied. The Ossimi and Rahmani sheep produce coarse wool. The reciprocal crosses had wool of coarser fibre than the two parent breeds.

ALTHOUGH the annual output of wool in Egypt amounts to 2,250,000 kg. it does not suffice for the increasing demands of the country. Moreover, the wool produced is of a coarse type which is mainly used for blanket and rug manufacture.

A crossbreeding experiment between two breeds of Egyptian sheep was carried out to study the effect of crossing on wool characteristics. The Ossimi and the Rahmani breeds, being the most popular, were chosen for this work. Staple length, fibre length, and fibre diameter of the parent-breeds and their F_1 crosses were studied.

Experimental Procedure and Methods

This experiment was carried out on the Experimental Farm of the Animal Breeding Department, Faculty of Agriculture, University of Cairo, Giza. It started in 1951 and ended in 1954.

The procedures of mating and management were according to those reported by Asker *et al.* [1], and the following four groups of lambs were obtained: (1) Pure Ossimi, (2) Pure Rahmani, (3) Crossbred lambs from Ossimi rams × Rahmani ewes, and (4) Crossbred lambs from Ossimi ewes × Rahmani rams. All animals used in this study were singles, and rams were not castrated. The sex ratio in groups at different ages was very close to 50 per cent. Most of the lambs were dropped within one month beginning in October.

Sheep are usually sheared twice a year in Egypt, in March and September, and samples were collected at those times, i.e. in October 1952, March 1953, and September 1953. The numbers of samples taken were 65, 58, 44, and 62 for the four groups of lambs in the order mentioned above.

Prior to shearing, a small sample of greasy wool was clipped from the

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right shoulder of each animal, using fine scissors. This sample was used to determine staple length, fibre length, and fibre diameter. For measuring staple length, the method suggested by Skinkle [2] was used. For fibre length and fibre diameter the methods used by Hunt *et al.* [3] were followed.

Means and standard errors of all measurements were calculated according to Snedecor [4], while the method of Cochran and Cox [5] was used for testing differences between and within groups.

Results and Discussion

Staple length.—The Ossimi group had the longest and the Rahmani the shortest staple (Table 1). The differences between the two groups were highly significant at all ages studied. Both types of crosses were intermediate in staple length between the two parent breeds. However, no significant differences in staple length were found between the crosses taken as one group and the pure breeds as another.

No significant differences were found between the reciprocal crosses at the different ages. Significant differences were observed between the pure Ossimi and each of the two crosses at 6, 17, and 23 months old, and between the pure Rahmani and each of the two crosses at the ages of 11 and 17 months.

Sex had a significant effect on differences in staple length between groups only at 6 months old. The shortest staple length among the four groups was obtained at 11 months old, and the longest at the age of 23 months.

The daily gain in staple length for the Ossimi group was approximately 0·5 and 0·6 mm. during the first and second years of age respectively, whilst that for the Rahmani sheep ranged between 0·4 and 0·5 mm. during the whole period. The crossbred animals were intermediate between the two pure breeds in this respect.

The total staple length of the Ossimi was 6·3 inches for the first 11 months' growth while it came to 8·9 inches for the next 12 months. The Rahmani group ranged from 5·3 to 6·4 inches. Kammlade [6] stated that the staple length was 3, 4, and 7 inches for Merino, Oxford, and Romney sheep respectively. Thus the Ossimi and Rahmani breeds can both be classified as long-wool types of sheep. Badreldin *et al.* [7] came to the same conclusion studying the Ossimi breed.

Fibre Length.—The Ossimi sheep had the longest fibre at 6, 17, and 23 months old, while the crossbred animals from Rahmani ewes had the longest fibre at the age of 11 months. The Rahmani group was the shortest in fibre at all ages (Table 1). The differences between Ossimi and Rahmani were highly significant.

The two types of crosses were intermediate between the two parent breeds at all ages except at 11 months. However, comparison between the crossbred groups taken as one unit and the purebred ones as another, did not show any significant difference except at 11 months. The two reciprocal crosses did not show significant differences at any age.

Significant differences between pure Ossimi and crossbred animals from Ossimi ewes were found only at 23 months old. There were no

significant differences between pure Ossimi and crossbred animals from Rahmani ewes at 6 and 11 months of age, but at 17 and 23 months old significant differences were found.

No significant differences were found between pure Rahmani sheep and either of the two types of crosses at 6 months old, while at 11, 17,

TABLE 1. *Mean Staple Lengths, Fibre Lengths and Fibre Diameters for Purebred and Crossbred Sheep at Different Ages*

Group	*No. of animals*	*Mean staple length (mm.)*	*Mean fibre length (mm.)*	*Mean fibre diameter (microns)*
At 6 months old:				
Ossimi	20	98·1 ± 4·4	107·8 ± 5·3	52·54 ± 0·64
Rahmani	17	81·8 ± 3·6	91·4 ± 3·8	24·72 ± 0·83
Oss. R. × Rahm E.	13	89·6 ± 4·6	102·4 ± 6·5	23·96 ± 0·61
Oss. E. × Rahm. R.	18	88·9 ± 4·2	101·8 ± 5·3	29·99 ± 0·81
At 11 months old:				
Ossimi	25	61·6 ± 2·2	66·6 ± 2·9	24·98 ± 0·59
Rahmani	21	51·6 ± 2·2	55·1 ± 2·9	24·02 ± 0·70
Oss. R. × Rahm. E.	17	60·2 ± 2·6	68·4 ± 2·8	26·61 ± 1·22
Oss. E. × Rahm. R.	25	57·8 ± 2·4	66·0 ± 2·3	28·00 ± 0·65
At 17 months old:				
Ossimi	10	110·3 ± 4·4	116·9 ± 5·9	33·46 ± 1·62
Rahmani	10	80·2 ± 3·1	90·0 ± 4·5	31·02 ± 0·71
Oss. R. × Rahm. E.	8	93·3 ± 5·5	102·2 ± 4·4	34·00 ± 1·39
Oss. E. × Rahm. R.	10	96·7 ± 3·7	111·4 ± 4·5	36·34 ± 1·19
At 23 months old:				
Ossimi	10	116·6 ± 9·1	127·0 ± 7·6	32·02 ± 0·81
Rahmani	10	82·9 ± 4·1	84·9 ± 4·7	29·27 ± 0·57
Oss. R. × Rahm. E.	6	100·2 ± 6·8	106·9 ± 6·9	32·78 ± 1·52
Oss. E. × Rahm. R.	9	104·0 ± 4·5	109·5 ± 4·9	35·53 ± 1·79

and 23 months old differences in this respect were significant. Sex had a significant effect upon fibre length as between the different groups only at 6 months old.

The shortest fibre length in all groups was at 11 months old, while the longest was at 23 months in the Ossimi group and the crossbred sheep from Rahmani ewes, at 6 months in the Rahmani sheep, and at 17 months for the crossbred sheep from Ossimi ewes.

The average fibre lengths for 12 months' growth for pure Ossimi, pure Rahmani, crossbred animals from Rahmani ewes, and from Ossimi ewes were higher than those reported by Hunt *et al.* [3] for Rambouillet, Black Top Delaine, and their F_1 hybrids respectively.

The relationship between the staple length and the fibre length indicates the amount of crimp in the wool. The study of this point showed that this ratio was over 92 per cent. for the two pure breeds. Hultz [8] with Rambouillet sheep, found a ratio of 66·5 per cent. It would thus appear that both Ossimi and Rahmani sheep have little crimp in their wool compared to improved breeds of sheep. Crossing appeared to have

a slight effect in increasing the crimp: the average ratio for the two crossbred groups was approximately 90 per cent.

This experiment thus showed that the crossbred animals were intermediate in staple length and fibre length between the two parent breeds and that the Ossimi were superior to the Rahmani sheep in those characters. Since long wool fibres appear to be dominant to shorter fibres [9], the intermediate values of staple and fibre length in the F_1 hybrids could be explained on the basis of gene interaction.

Fibre diameter.—The Rahmani sheep had the finest fibre while the crossbred animals from Ossimi ewes had the coarsest at all ages as did also the reciprocal cross except at 6 months. Highly significant differences were found between the Rahmani group and the crossbred animals from Ossimi ewes, at all ages. Between the two reciprocal crosses there was a highly significant difference only at 6 months. Sex had no significant effect upon fibre diameter between groups at any age.

The Ossimi and the Rahmani groups produced their finest fibre at 11 months, and the coarsest at 17 months. Both of the crossbred groups had their coarsest fibre at 17 months; the finest fibres in these groups were found at 6 and 17 months for the animals sired by Ossimi and Rahmani rams respectively.

The Ossimi and Rahmani breeds, with fibre diameters of 24–25 microns in the first year and 30–32 microns in the second year are coarse-wool sheep compared with breeds such as Rambouillet, for which Jones *et al.* [10] found fibre diameters of 11·8 and 13·2 microns in the first and second years of age.

As the sheep of all four groups in these experiments grew older the fibre diameter gradually increased. Jones *et al.* [10], studying the Rambouillet breed, and Badreldin *et al.* [7], working on Ossimi sheep, similarly found that age had a considerable effect on the fineness of the wool.

Each of the reciprocal crosses had coarser fibre than either of the parent breeds at all ages studied, except at 6 months. Since coarser fibres are less desirable, this may be described as a negative heterosis. Hunt *et al.* [3], studying the effect of crossing Rambouillet with Black Top Delaine sheep, came to the same conclusion. They found an average fibre diameter of 20·61 microns for the F_1, compared with 18·11 and 17·75 microns for Rambouillet and Black Top Delaine respectively. Since coarseness of fibre is dominant [9], either the dominance or the gene-interaction hypothesis of heterosis can explain this observation.

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GRAZING BEHAVIOUR TESTS WITH MAURITIUS CREOLE COWS

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Summary

The grazing behaviour of Mauritius Creole cows is described with regard to the effects of air temperatures between 68 and 84° F. and coat colour.

Increasing temperatures reduced the percentage 'working time' of the animals, and 80 to 81° F. is shown to be a critical point in this effect.

There was a connexion between coat-colour groups and grazing behaviour, but this is shown to be independent of the reaction of the animals to air temperature.

In field tests carried out at the Mauritius Government Stock Breeding Centre at Palmar in the summer of 1951–2 animals of the Mauritius Creole Breed of Milch Cattle showed themselves to be more heat-tolerant than local-bred Friesians and Friesian/Creole crosses [1]. Their coefficient of heat tolerance, as defined by Rhoad [2], was higher and their milk production less adversely affected by high air temperatures.

As it was not possible to study grazing behaviour at the time, the field tests described here may be regarded as a continuation of those at Palmar and a further step in the study of the Creole Breed.

Material and Design

Six mature pregnant Creole cows in milk were used, three pigmented and three white but otherwise taken at random. All had short hair, smooth coats, and thin skins. Judged by its appearance and according to its history the Creole is pure *Bos taurus* [1].

Although dairy cows are stall-fed in Mauritius these six cows had been accustomed to grazing for a portion of each day and to receiving a supplementary ration of concentrates at the morning (6 a.m.) and afternoon (3 p.m.) milkings at the rate of 1 lb. per day for each 2·7 lb. of milk produced.

The pasture, situated in the grounds of Government House, Le Reduit, was divided by electric fencing into paddocks of a quarter to half an acre depending on the length and density of the herbage. Each paddock had varying amounts of tree shade. The dominant grass was *Stenotaphrum dimidiatum* with an admixture of *Paspalum paniculatum*, and the grazing would be classified as 'poor' in the scale adopted by Hancock [3].

Management was adjusted to provide a daily herbage offering as uniform as possible. Water was available at all times.

The cows received no fodder in the stable and were put out to grass from 9 a.m. to 2 p.m. except on Sundays and when rain was falling. It was found in preliminary trials that after 2 p.m. the animals tended to 'idle' at the gate awaiting their return to the stable.

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The trials extended over three periods in the first half of 1955, namely 14 days in March, 12 in May and early June, and 11 days in late June; a total of 37 days on which recordings were made.

Tests were carried out for the first 6 days of the trials with benzene hexachloride and D.D.T. sprays as deterrents against biting flies of Stomoxys spp., mainly *S. nigra*. In these tests the cows were divided into three pairs, each consisting of a pigmented and a white animal. One pair was sprayed with benzene hexochloride (0·1 per cent. gamma isomer) each day shortly before going out to grass; another pair with D.D.T. (2 per cent.), and the third pair, unsprayed, was retained as control.

Recordings

The following recordings were made.

(i) *Grazing behaviour*. The activities of each animal while at grass were recorded at 5-minute intervals. A simplified form of the nomenclature suggested by Hancock [3] was used, viz.: '*Working time*' is the sum of the periods spent in grazing and rumination, and includes short periods of walking while selecting grass. '*Idling time*' is that portion of the time at grass not spent in 'working', and consists of walking when not grazing, and standing and lying down when not ruminating.

(ii) *Milk Production*. The daily milk production of each animal had been recorded since calving, and this practice was continued throughout the tests. Milk yield was used as a measure of sufficiency of herbage intake.

(iii) *Air temperature* was recorded on a bare Fahrenheit thermometer suspended in shade 4 feet above dense sward in the paddock where the cows were grazing. Readings were taken at the same 5-minute intervals as the observations on the grazing behaviour.

(iv) *Air movement*. The approximate strength and direction, gauged without instruments, were noted for each grazing period.

(v) *Relative humidity* was recorded at infrequent and irregular intervals in each grazing period.

(vi) *Body-weight of animals*. The weight of each cow was estimated from heart girth at the start of the tests, using Kendrick and Parker's table [4].

(vii) *Stomoxys flies*. Counts of the number of flies on the proximal side of each animal were made at half-hourly intervals.

Results and Observations

Grazing behaviour.—The manner in which the cows spent the time at grass over the whole test is indicated in Table 1. Two thousand observations were recorded for each animal.

No differentiation has been made between 'idling' in the sun and in the shade. Examination of the 'idling time' of all the cows over the 14 days in March showed that slightly less time was spent in the shade than in the sun, which would appear to indicate that Creoles are not greatly affected by differences between sun and shade at the air temperatures encountered over that period, that is 76 to 84° F. Indications of this had

appeared in heat-tolerance tests carried out by the author at Palmar in 1951/2. For this reason, and because the weather was appreciably cooler in May and June and the available grazing more shaded, no further distinction was made between the idling time spent in the sun and that spent in the shade.

While it was realized that the effects on the cows of changes in air

TABLE 1. *Time at Grass spent in 'Working', in relation to Air Temperature. Average percentages*‡

	Environmental temperatures (°F.)																
	68°	69°	70°	71°	72°	73°	74°	75°	76°	77°	78°	79°	80°	81°	82°	83°	84°
Three pigmented cows	97	94	96	94	92	93	91	88	85	86	89	90	84	76	73	74	67
Three white cows .	92	91	90	89	86	86	81	82	78	77	70	73	74	61	64	61	58
All cows . . .	94	92	93	91	89	89	86	85	81	82	80	81	79	69	68	67	63

‡ Rounded to nearest whole number.

temperature would often be carried over to the subsequent 5-minute period it was decided that the general pattern of results would not be materially affected.

Periods at grass when rain was falling have been discarded in assessing results, for if the animals were grazing they usually stopped to take shelter or to stand with their tails to the weather.

TABLE 2. *Analysis of Variance of Data summarized in Table 1*
(rounded to one decimal place)

Factor	*Degrees of freedom*	*Sum of squares*	*Variance*	*Variance ratio*
Temperature . .	16	9466·4	591·7	14·9†
Colour	1	2174·9	2174·9	54·9†
Colour × Temp. . .	16	468·9	29·3	1
Error	69	2732·7	39·6	..
Total . . .	102	14842·9	..	..

Difference between means for coat colour: 9·3*.
Minimum significant difference ($t = 2$ approx.) for *Temperature* = 7·3.
for *Coat colour* = 2·5.

* $P < 0.05$. † $P < 0.01$.

The analysis of variance of the data from this experiment (Table 2), shows that there was a highly significant effect of environmental temperature and of coat colour on percentage working time of the animals at grass.

However, when the changes in ambient air temperature are considered in steps of 1° F., only the change from 80 to 81° F. (10 per cent.) resulted in a significant effect on grazing behaviour.

This suggests that 80 to 81° F. may be a critical air temperature in respect of the grazing behaviour of Creole cows in milk.

White animals spent a significantly lower proportion of their time at grass in 'working'. The interaction between coat colour and temperature was not significant, indicating that the different grazing behaviour of

the coat-colour groups was not connected with different responses for coat colour to variations in temperature. As two of the white cows were temperamentally restless and easily diverted from grazing by objects of interest such as passing traffic, and were usually the first to make a move in a homeward direction in the afternoons, it is thought that this difference in behaviour was connected with temperament or with a smaller herbage requirement. Their condition remained excellent throughout the tests.

TABLE 3. *Ranges and Means of Air Temperatures* (°F.)

	14 days in March	*12 days May/June*	*11 days late June*	*37 days over whole test*
Temperature range	76–84	72–76	68–71	68–84
Mean temperature	80·4	73·6	69·8	75·1

Milk production.—The milk yields of the cows followed the normal lactation curve for Creole cows [1] throughout the tests. This was taken as an indication of the sufficiency of the herbage intake.

Air temperatures.—Table 3 gives the ranges and means of temperatures recorded.

TABLE 4. *Mean Air Temperatures from Hour to Hour* (°F.)

	14 days in March	*12 days May/June*	*11 days late June*	*37 days over whole test*
9 a.m. to 10 a.m.	79·2	71·7	69·1	73·8
10 a.m. to 11 a.m.	80·7	73·1	70·3	75·2
11 a.m. to noon	80·8	73·9	70·1	75·4
Noon to 1 p.m.	80·7	74·8	69·8	75·5
1 p.m. to 2 p.m.	80·8	74·7	69·6	75·5

Had the higher air temperatures encountered in these tests been confined to the latter portions of the grazing periods, as might reasonably have been expected, it could have been argued that any reduction of 'working time' at the higher temperatures could have been caused partly by a lessening of appetite as satiety was approached. It is, however, clearly shown in Table 4 that this was not the case, as there were no appreciable differences in the mean temperatures for each hour after 10 a.m.

Air movement.—The strength of air movement was usually No. 2 to No. 3 on the Beaufort scale, that is, light to gentle breeze, with occasionally Nos. 4 and 5, moderate to fresh breeze, and, more rarely, short periods of calm.

Relative humidity.—The mean of the relative humidities recorded was 70 per cent.—too low to have any marked physiological effect on cattle at the air temperatures under discussion, as had been indicated in heat-tolerance tests at the Palmar Stock Breeding Centre in 1951/2 (unpublished data). This accords with the findings of Findlay [5].

Body-weight.—It was shown that the heavier animals spent no more of their time at grass in 'working' than the lighter ones.

Stomoxys flies.—Results were altogether inconclusive. Although it was not possible to obtain exact counts of the flies on the animals, on account of their constant coming and going, there were no indications that either of the sprays exerted a deterrent effect, or that the flies showed any preference for the dark- or the light-coloured animals.

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A MECHANICAL SIEVE DESIGNED FOR EXPERIMENTAL WORK ON TILTHS

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WITH PLATE 8

Summary

A rotary sieve is described which can separate soil into five particle-size groups simultaneously at a rate of about 7 lb./min. under suitable conditions. The reliability of the separation data derived from the work of the machine is demonstrated.

THE influence of the seed-bed on the development of crop plants, although obviously a fundamental problem in crop husbandry, has not, in itself, been the subject of any considerable body of experimental work. The difficulty of finding any accurate method of measuring and describing a 'tilth' has been, and still is, one of the chief obstacles and much of the research endeavour in this field has concerned itself with physical determinations attempting to establish standards for comparing one soil condition with another. Attempts to answer the question 'How do plants respond to measurable structural differences in the seed-bed?' have been made along three main lines:

(i) Surveys conducted on actual farm crops where an attempt has been made to estimate the character of the seed-bed and then to relate the subsequent yield to this seed-bed character [1].

(ii) Field experiments in which attempts have been made to produce a series of seed-beds with different characteristics by differential cultivations and then the crop has been superimposed on this pattern and studied [2, 3, 4, 5].

(iii) Experiments in pots on small plots where seed-beds have been made up of soil aggregates, and solid particles of known size range, these having been separated by some sieving process [6, 7, 8, 9].

Each of these approaches has obvious disadvantages which it is not within the scope of this paper to discuss.

The mechanical sieve here described has been designed to facilitate experimental work of the type outlined in (iii) above. One of the difficulties in the preparation of seed-beds from separates of known size range is the great weight of soil which has to be handled and sieved. Kvasnikov [7] and Hagin [9] have circumvented this difficulty by using pots which contain relatively small quantities of soil. Difficulties associated with border effects, propinquity, and watering régime are inherent in pot work and make it difficult to relate the results to field conditions. Yoder [8] has used field plots but economized in soil by dispensing with replication and was, therefore, unable to make any valid estimate of the experimental error. The mechanical sieve described here has made it possible to treat enough soil to provide seed-beds large enough to allow some discard for border effects and yet to adopt a sound statistical layout.

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The Mechanical Sieve

Rotary screens of this type have been employed in quarries and gravel pits for grading sand and ballast for many years. Chepil and Bisal [10] have described a small rotary analysing sieve designed by them to carry out routine mechanical analysis and Chepil [11] a more intricate development of this machine. These are essentially laboratory tools designed for the accurate separation of small quantities of oven-dried soil. It was thought that a rotary sieving machine intermediate in size and complexity between the extremes cited above might prove a valuable tool in the preparation of experimental seed-beds.

It is more consistent, less abrasive, and less laborious than hand sieving and has a higher output than mechanical sieves of the high-frequency vibration type described by Brown, Fountaine, and Payne [12].

A general view of the machine is given by Plate 8 and details of the construction in Figs. 1 and 2.

The sieve consists of concentric cylinders of mild steel each of which incorporates a cylindrical screen. The cylinders are assembled in such a way that the screens are arranged in echelon in order of size of aperture from largest to smallest outward and downward. The screens are interchangeable and any appropriate mesh can be fitted. The screening rotor is mounted on a 1 in. steel shaft running in bearings fixed to a welded tubular steel frame which has adjustable legs at the feed end, permitting variation in the angle of slope of the screens. This angle controls the speed at which soil passes across the screens. The normal inclination is 5° from horizontal. Motive power is provided by a $\frac{1}{3}$ h.p. electric motor which runs at 1,440 r.p.m. A worm-type reduction gear-box and suitable V-belt pulleys give a final drive speed of 14 r.p.m. The feed mechanism is of the usual jog-tray type actuated by a four-lobed cam and lever. The rate of feed can be easily, and very accurately, adjusted by varying the tension of the return spring and by altering the slope of the jog tray. The hopper has a cut-off slide at its base. At the delivery end, chutes collect the separates and deliver them into suitably placed trays. The finest sieve is kept clear by a revolving brush and also by a mechanism which taps the wire mesh four times per revolution.

Operation and Use of the Machine

The machine can separate soil fed into the hopper into five separates at a normal speed of about 7 lb./min. Provided that conditions are favourable, one man can sieve about a ton of soil in an 8-hour day. It should be noted, however, that the soil has first to be passed through a coarse hand screen to remove large stones and trash. The size of the apertures of this screen controls the upper size limit of the material passed out of the central cylinder.

The efficiency of separation depends on:

(i) the moisture content of the soil;
(ii) correct setting of the sieve controls in relation to (i);
(iii) cleaning of the screens at appropriate intervals.

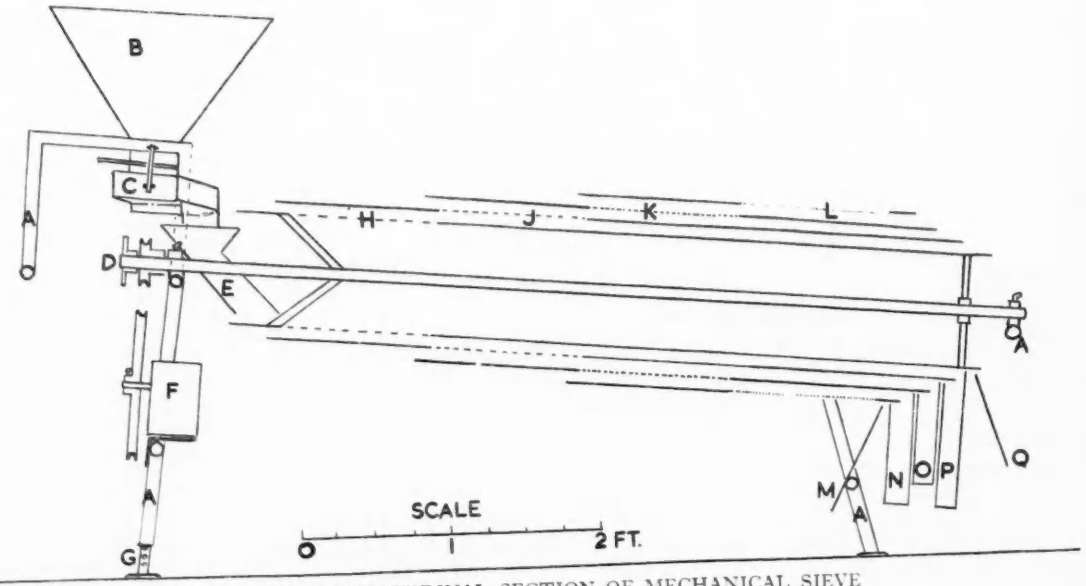

FIG. 1. DIAGRAMMATIC LONGITUDINAL SECTION OF MECHANICAL SIEVE

KEY

A Tubular frame
B Hopper 60 lb. capacity
C Jog tray
D Main shaft, V-belt pulley, and jog cam
E Feed chute
F Motor, gear box, and drive pulley
G Extending leg
H Perforated plate, $\frac{1}{2}$" round holes
J Perforated plate, $\frac{1}{4}$" round holes
K " " $\frac{1}{8}$" " "
L Woven wire 1 mm. square holes
M Chute for separates < 1 mm
N Chute for separates 1 mm.
O " " " "
P " " " "
Q " " " "

As with all methods of sieving soil in air, the higher the moisture content the more difficult it becomes to achieve efficient separation. The influence of this factor on the results of hand sieving have been investigated by Russell and Tamhane [13]. Above a critical moisture content, which varies from one soil to another but is, in this case, about 35 per cent., sieving becomes impossible as the soil balls on the screens. The sieve

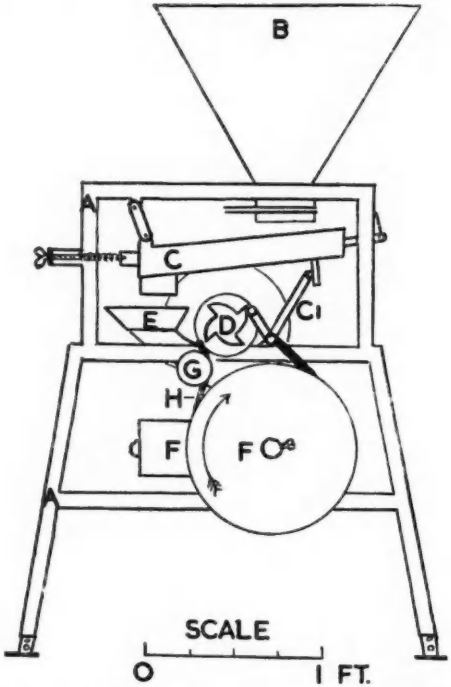

FIG. 2. DIAGRAMMATIC VIEW OF FEED END

KEY

A	Tubular frame	C1	Jog tray connecting link	F	Motor, gear box, and pulley
B	Hopper	D	Jog cam on main shaft	G	Spring-tensioned jockey pulley
C	Jog tray with return spring	E	Feed chute	H	V-belt

here described has certain advantages over reciprocating sieves of the usual type when the soil is damp because:

(i) only a very thin layer of soil is on the screens at any one time; this reduces the scrubbing action inherent in a reciprocating screen;

(ii) control of the rate of feed is much easier. By reducing the angle of the screens and lowering the feed rate, efficient separation can be achieved on soils which, by reason of their high moisture content, are not amenable to hand sieving. This is particularly true of the finer screens.

It must be noted, however, that in the work in which the sieve is at

present used, it is not desirable to take advantage of this capacity of the machine to cope with damp soil.

One measure of the efficiency of the machine is its capacity to give consistent results when samples drawn from a given soil are fed to it for separation. The results of one such test given in Table 1 show that, provided the sampling technique is sound and the moisture content of the soil within the critical range, the dispersion around the mean is very small. For comparison Table 1 also includes data obtained from a nest of 8 in.-diameter test sieves with similar apertures.

TABLE 1. *Particle Size Distribution in a Given Soil as Determined by Mechanical and Hand Sieving (Moisture content of soil: 15·3 per cent.)*

Method of separation		*Percentage of particles within fraction*				
		1 mm.	*1 mm.–$\frac{1}{8}$″*	*$\frac{1}{8}$″–$\frac{1}{4}$″*	*$\frac{1}{4}$″–$\frac{3}{8}$″*	*$\frac{3}{8}$″–$\frac{1}{2}$″*
Mechanical	Mean of 4 × 20 lb. samples	18·4	20·3	27·9	19·5	13·9
	S.E.±	0·10	0·31	0·58	0·56	0·36
Hand sieve	Mean of 6 × 200 gm. samples	17·0	20·9	26·6	21·4	14·1
	S.E.±	1·41	0·81	1·17	0·99	1·16

A second method of testing the work of the mechanical sieve involves passing the separates delivered by it through a nest of test sieves with apertures corresponding to those of the machine screens. The results obtained depend to a marked degree on the hand-sieving techniques employed [13]. It has been found necessary to adopt a standard method

TABLE 2. *Particle-size Distribution within Mechanically Sieved Separates (Mean moisture content of machine samples: 14·3 per cent.)*

Separates from machine within size ranges:	*Percentages of particles within size ranges: Means of three 200-gm. air-dry samples, hand sieved*									
	<1 mm.		*1 mm.–$\frac{1}{8}$″*		*$\frac{1}{8}$″–$\frac{1}{4}$″*		*$\frac{1}{4}$″–$\frac{3}{8}$″*		*$\frac{3}{8}$″–$\frac{1}{2}$″*	
	Mean	*S.E.±*	*Mean*	*S.E.±*	*Mean*	*S.E.±*	*Mean*	*S.E.±*	*Mean*	*S.E.±*
<1 mm. . .	100	..	..	..	..	..	..	..	..	..
1 mm.–$\frac{1}{8}$″ .	2·6	0·36	97·4	..	..	..	..	..	..	..
$\frac{1}{8}$″–$\frac{1}{4}$″ . .	0·5	0·0	7·2	1·37	92·3	..	..	..	..	..
$\frac{1}{4}$″–$\frac{3}{8}$″ . .	0·5	0·0	0·4	0·08	11·7	1·08	87·4	..	..	..
$\frac{3}{8}$″–$\frac{1}{2}$″ . .	0·4	0·0	0·3	0·05	1·1	0·19	13·7	0·65	84·5	..

which in practice has given results with a reasonably small dispersion. The results of one such test are given in Table 2, while the effect of higher moisture content on the efficiency of separation is shown when Table 3 is compared with Table 2.

It will be noted that, of the particles which fall outside the expected size range, a high proportion fall within the size range next smaller than the expected one. This is not surprising when the importance of the orientation of irregularly shaped particles is taken into account. Irregularities of distribution of the kind shown in Tables 2 and 3 have not, at any time,

become sufficiently serious to cause difficulties in the experiments in which the sieve is used. It has, in fact, given reliable service for two years and has sieved many tons of soil. It is hoped to publish the main experimental results at a later date.

TABLE 3. *Particle Size Distribution within Mechanically Sieved Separates (Mean moisture content of machine samples: 31·2 per cent.)*

Separates from machine within size ranges:	*Percentages of particles within size ranges: Means of three 200-gm. air-dry samples, hand sieved*									
	< 1 mm.		1 mm.–$\frac{1}{8}$″		$\frac{1}{8}$″–$\frac{1}{4}$″		$\frac{1}{4}$″–$\frac{3}{8}$″		$\frac{3}{8}$″–$\frac{1}{2}$″	
	Mean	*S.E.* ±	*Mean*	*S.E.* ±	*Mean*	*S.E.* ±	*Mean*	*S.E.* ±	*Mean*	*S.E.* ±
< 1 mm. . .	100	..	..	..	..	..	..	..	..	..
1 mm.–$\frac{1}{8}$″ .	6·0	0·14	94·0	..	..	..	..	..	..	..
$\frac{1}{8}$″–$\frac{1}{4}$″ . .	1·2	0·22	8·2	1·09	90·6	..	..	..	..	..
$\frac{1}{4}$″–$\frac{3}{8}$″ . .	1·3	0·19	1·7	0·14	10·9	0·22	86·1	..	..	..
$\frac{3}{8}$″–$\frac{1}{2}$″ . .	2·0	0·52	1·2	0·38	1·8	0·19	16·6	1·53	78·4	..

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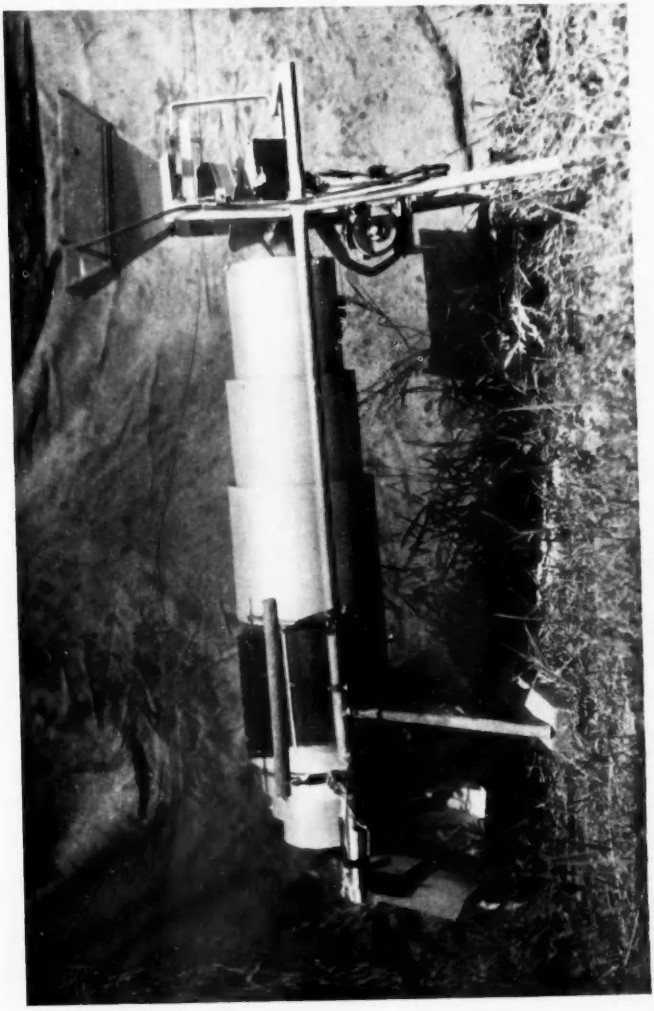

MACERATED DATES AND GROUND DATE STONES AS FEEDS FOR FATTENING SHEEP

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Summary

Two feeding trials involving 156 yearling sheep were carried out to determine the practicability of replacing a portion of the ground barley in the fattening ration by macerated dates or ground date stones. Date stones were prepared by grinding in a burr mill. They could be mixed easily with concentrate-feed ingredients such as ground barley and sesame-seed-oil meal. Macerated dates were prepared by putting whole dates through a special macerator which removes the stones. The sticky mass of date meat was then mixed with ground barley in a special mixing machine such as is used in commercial bakeries for mixing dough. Various mixtures ranging in composition from 17 up to 85 per cent. of macerated dates or ground date stones were eaten readily. No digestive disturbances associated with the date feeds were noted. When properly supplemented with protein, in which both macerated dates and date stones are rather low, the date feeds produced very satisfactory and economical rates of gain.

THE feeding of dates and date stones to livestock, especially sheep and cattle, is an extremely old practice in Iraq. Nomadic shepherds from southern Iraq often carry quantities of dates for sheep feed as they leave the valley for the desert in the winter and spring. The dates are used as a reserve feed if the rainfall happens to be inadequate for sufficient growth of range plants. Date stones, soaked until soft, are fed extensively by sheep feeders in certain southern towns where most of the dates are grown. Considerable quantities of stones are exported to the Persian Gulf countries for the same purpose.

Some varieties of dates are naturally so inferior in quality that they command only very low prices. In the date-packing plants significant quantities of culled dates, also low in price, accumulate. The price of low-quality dates may be much below that of barley, the standard livestock concentrate feed of the country. Sometimes a ton of low-quality dates will sell for less than half the price of a ton of barley. It is estimated that not less than 70,000 metric tons of low-quality dates, culled dates, date stones, and date marc are available in Iraq annually. This difference between the prices of low-quality dates and barley justifies an experimental study of the feeding of low-quality dates.

Apparently little experimental investigation of the feeding of dates and date stones has been attempted. In a previous experiment Sarsam, Ali, and McLeroy [1] found that macerated dates (dates from which the stones have been removed), soaked date stones, and ground date stones fed without mixing with other feeds are consumed by yearling sheep only in small quantities not exceeding 1 lb. a day. When macerated dates or date stones were fed with only cereal straw as a roughage, the animals lost weight. This work suggested that the dates or date stones

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must be combined with other feeds in order to obtain a good level of consumption and at the same time secure a satisfactory rate of live-weight gain. The limited number of chemical analyses available (Table 1) show the protein content of date stones, and especially macerated dates, to be well below that of barley, thus pointing to the need for the inclusion of a protein-rich concentrate. The present investigation was concerned with finding a practicable way to substitute macerated dates or ground date stones for a portion of the barley which is normally used in the fattening ration of sheep.

Experiment 1

One hundred and twenty long-yearling (about 14 months old) male sheep of the fat-tailed Awasi breed were divided into eight lots of fifteen. The animals were so allocated to the lots that the average initial weight in each lot was just over 69 lb. Prior to being placed on feed, the animals were treated for liver fluke. Afterwards they were given phenothiazine for the control of other parasites.

Four of the lots received barley straw, the usual roughage fed to sheep in this country. The other four lots received green lucerne soilage. In each of these groups the following concentrates were fed:

Lot (1) Ground barley—100 per cent.; 9·00 per cent. crude protein.

,, (2) Ground barley—66 per cent.
Macerated dates—34 per cent. } 6·82 per cent. crude protein.

,, (3) Ground barley—53 per cent.
Macerated dates—34 per cent.
Sesame-seed-oil meal—13 per cent. } 10·46 per cent. crude protein.

,, (4) Ground barley—66 per cent.
Macerated dates—17 per cent.
Ground date stones—17 per cent. } 7·40 per cent. crude protein.

Table 1 gives the chemical analyses of the concentrates fed, from which were calculated the crude protein percentages of the mixtures as indicated above.

Macerated dates were prepared at the date-packing plant of the Date Association at Baghdad. The macerating machine rapidly removes stones from the whole dates, leaving the date meat. Dried date stones were ground to a medium degree of fineness in a burr mill. Choice of the proportions of dates or date stones to use in the concentrate mixtures was largely arbitrary. It appeared desirable to substitute these feeds for barley at a substantial rate; the level of about one-third dates or date products was therefore chosen. Sesame-seed-oil meal was included in one mixture to improve the palatability and to increase the protein content to equal or slightly exceed the protein content of barley.

At first the experimental feeds were mixed in the plant of the Date Association in Baghdad, using the Hobart mixing machine. Although it may be too small for commercial-scale feed mixing, this machine is excellent for blending macerated dates with ground barley. Ground barley and ground date stones appear to act as abrasives, tearing the

macerated dates into such small fragments that they are hardly detectable in the mixture. The finer particles of ground barley stick to the date fragments, making them dry and flaky. The feed can be poured quite easily from a bag.

TABLE 1. *Chemical Composition of Concentrates*

Feed	*Number of samples averaged*	*Dry matter* %	*Crude protein* %	*Crude fat* %	*Crude fibre* %	*N-free extract* %	*Mineral matter* %
Macerated dates	1	79·5	2·6	0·5	3·4	70·8	2·2
Ground date stones	2	91·1	6·0	7·2	14·7	60·1	3·1
Ground barley	2	90·4	9·0	1·0	5·0	72·4	3·0
Sesame-seed-oil meal	2	92·3	37·0	6·8	5·4	27·7	15·4

Results.—The sheep very readily consumed the different mixtures. There were no difficulties in getting them on feed and there were no severe digestive upsets. Perhaps undue caution was used in getting the

TABLE 2. *Average Gains in Weight (unweighted means) of Yearling Awasi Rams Fed for 84 Days on Two Roughages in Combination with Four Concentrate Mixtures. Pounds per sheep*

(Numbers in parenthesis are numbers of animals which finished the trial)

Concentrate	*Barley Straw group*	*Green lucerne group*	*Average*
Ground barley, 100%	(15) 22·40	(14) 33·70	28·05
Ground barley, 66% Macerated dates, 34%	(12) 16·25	(13) 33·15	25·70
Ground barley, 53% Macerated dates, 34% Sesame-seed-oil meal, 13%	(12) 27·50	(15) 35·87	31·68
Ground barley, 66% Macerated dates, 17% Ground date stones, 17%	(14) 14·50	(13) 33·46	23·98
Average	20·16	34·54	

sheep on feed, in the four green lucerne lots. It was expected that there would be some cases of diarrhoea if green lucerne were increased too rapidly and simultaneously with increase in the concentrates in the date-feed lots; consequently, feed increases were made so slowly that the four lots gained practically nothing in the first 14 days of the trial. Later experience suggests that the increase of both the green alfalfa and concentrates could have been made more rapidly with little danger to the animals.

The average gains in weight per sheep for the eight groups are given in Table 2.

Five of the experimental animals died. Seven more were removed

from the experiment because they were sick or so generally unthrifty that they could not compete at the feed trough. It is believed that the deaths or unthriftiness were due to the fluke infestation or other parasites.

The erratic losses of animals from the experiment resulted in disproportionate numbers in the lots. The method described by Snedecor [2] for treating disproportionate subclass numbers in an R × 2 table was used and the completed analysis of variance is given in Table 3. From the analysis of variance of individual gains it can be seen that the difference in roughages, as of course was expected, was one of the major

TABLE 3. *Analysis of Variance of Individual Gains—Original Data*

Source	Degrees of freedom	Sum of squares	Mean square
Total	107	12446·9	
Subclasses (lots)	7	7089·1	
Roughages	1	5679·8	5679·8
Concentrates	3	1042·0	347·3
Individuals	100	5357·8	53·6

Analysis of Variance of Individual Gains Treated for Disproportionate Subclass Numbers—Interaction Present

Source	Degrees of freedom	Sum of squares	Mean square
Total	107	12446·9	
Roughages	1	5547·2	5547·2†
Concentrates	3	888·0	296·0†
Interaction	3	578·0	192·7*
Individuals	100	5357·8	53·6

* $P < 0.05$. † $P < 0.01$.

sources of variation. There was a significant difference in the mean gains produced on the different concentrate mixtures ($P < 0.01$), but this does not show whether there was a real difference between the date feeds and barley. By rearranging the data in three 2 × 2 tables (Table 4) and again using the method described by Snedecor for treating the bias caused by disproportionate subclass numbers (Table 5), it is possible to get a better insight into the results obtained with the concentrates.

Table 6 summarizes the average daily feed consumption in the different groups. The maximum daily consumption of concentrates was 2 lb. an animal. Thus the animals receiving the date feeds each ate 0·68 lb. of macerated dates or macerated dates plus date stones a day during part of the feeding period.

Experiment 2

When it became apparent that sheep would eat with good appetite the concentrate mixtures with 34 per cent. dates or dates and date stones, another smaller-scale trial was started. Its purpose was mainly

TABLE 4. *Comparison of Average Weight Gains of Groups of Yearling Awasi Males. Pounds per animal.*

(Numbers in parenthesis are numbers of animals which finished the trial)

Concentrates	*Barley straw group*	*Green lucerne group*	*Unweighted means*
(1) *Barley* v. *date feeds:*			
Barley	(15) 22·4	(14) 33·7	28·1
Date feeds	(38) 19·2	(41) 34·9	27·0
Difference	3·2	−1·2	1·1
(2) *Date stones* v. *no date stones:*			
Date stones	(14) 14·5	(13) 33·5	24·0
No date stones	(39) 22·1	(42) 34·9	28·5
Difference	−7·6	−1·4	−4·5
(3) *Sesame-seed-oil meal* v. *no sesame-seed-oil meal:*			
Sesame-seed-oil meal	(12) 27·5	(15) 35·9	31·7
No sesame-seed-oil meal	(41) 17·9	(40) 34·1	26·0
Difference	9·6	1·8	5·7

TABLE 5. *Analysis of Variance of Individual Gains*

Source	*Degrees of freedom*	*Sum of squares*	*Mean square*
Roughages	1	5547·2	5547·2†
Barley *v.* date feeds	1	21·3	21·3
Interaction with roughage	1	103·5	103·5
Date stones *v.* no date stones	1	422·8	422·8†
Interaction with roughage	1	189·2	189·2
Sesame oil meal *v.* no sesame oil meal	1	648·6	648·6†
Interaction with roughage	1	307·4	307·4*
Individuals	100	5357·8	53·6

Note. The sums of squares associated with the individual degrees of freedom for each of the three comparisons are not additive because all the data were used each time a sum of squares was calculated for an individual comparison.

* $P < 0.05$. † $P < 0.01$.

TABLE 6. *Average Daily Feed Consumption (pounds per animal)—Experiment 1*

	Barley straw groups		*Green lucerne groups*	
	Concentrate	*Roughage*	*Concentrate*	*Roughage*
Ground barley	1·7	1·0	1·7	4·9
Ground barley, 66% Macerated dates, 34%	1·7	1·1	1·7	5·2
Ground barley, 53% Macerated dates, 34% Sesame-seed-oil meal, 13%	1·7	1·2	1·7	4·8
Ground barley, 66% Macerated dates, 17% Ground date stones, 17%	1·7	1·0	1·7	5·1

to determine whether sheep would eat certain mixtures with higher proportions of dates or date stones. Five lots, each of six yearling Awasi ewes, were fed on different concentrate mixtures containing high proportions of dates or date stones for a period of 91 days (19 March to 18 June 1955). The roughage was barley straw and green lucerne soilage. A sixth lot of six ewes were given no concentrates, but were allowed to eat all the roughage they wanted. The first five lots were brought rapidly up to a full feed of concentrates, which was 2 lb. an animal daily. The results of this experiment are given in Table 7. The

TABLE 7. *Gains of Awasi Ewes fed High Proportions of Macerated Dates and Ground Date Stones—91-day period*

Lot no.	*Concentrate mixture*	*Crude protein %*	*Average gain lb.*
(1)	45 per cent. macerated dates 45 per cent. ground barley 10 per cent. sesame-seed-oil meal	8·9	30·1
(2)	45 per cent. ground date stones 45 per cent. ground barley 10 per cent. sesame-seed-oil meal	10·4	33·9
(3)	50 per cent. ground date stones 30 per cent. macerated dates 10 per cent. ground barley 10 per cent. sesame-seed-oil meal	8·4	31·4
(4)	85 per cent. macerated dates 15 per cent. sesame-seed-oil meal	7·8	25·6
(5)	85 per cent. ground date stones 15 per cent. sesame-seed-oil meal	10·6	33·4
(6)	No concentrates	..	17·2

group which received the mixture containing 85 per cent. macerated dates and 15 per cent. sesame-seed-oil meal was often slow about eating the feed, as compared with the other groups, but even this group would finish all of its feed later in the day. No digestive disturbances were noted.

One ewe in Lot 2 was pregnant and was excluded from the data; the average of Lot 2 is based on the remaining five animals. In Table 8 is an analysis of variance of the gains in weight of the thirty-five animals in this second trial.

Discussion

Macerated date feeds.—Because of the low cost of dates in relation to the cost of barley, one of the main problems in view is the extent to which macerated dates can replace barley as a concentrate for fattening sheep. In every case where the date feeds appear to have been adequately supplemented with protein they compared very favourably with barley. Particularly did the date feeds give satisfactory results when the roughage was the protein-rich lucerne soilage (Table 2).

In the overall comparison of barley and the date feeds (Tables 4 and 5)

the difference of 1·03 lb. in average gain per animal in favour of the barley is not significant.

The date feed containing sesame-seed-oil meal produced an average gain significantly higher by 5·68 lb. than the non-sesame feeds (Tables 4 and 5). In the barley-straw lots the difference was 9·60 lb. in favour of the sesame-seed-oil meal, but it was only 1·77 lb. in the green-lucerne lots; this interaction was significant at the 5 per cent. level. Apparently the date feeds would be of the greatest value when fed with a protein-rich roughage.

It may be possible to feed proportions of dates higher than the 34 per cent. in the concentrate mixture fed in the first experiment. This possibility is suggested by the results of the second trial in which a mixture containing 45 per cent. macerated dates (in Lot 1) producing an

TABLE 8. *Analysis of Variance of Individual and Lot Gains*

Source	*Degrees of freedom*	*Sum of squares*	*Mean square*
Total	34	2014·5	
Lots	5	1173·1	234·6†
Regression of lot mean gains on protein percentages	1	1081·1	1081·1†
Difference for testing significance of lot mean gains	4	92·0	23·0
Individuals	29	841·4	29·0

† $P < 0.01$.

average of 30·1 lb. of gain, a fairly satisfactory gain considering that some of the daily maximum temperatures were exceeding 105° F. during the last month of the trial. In Lot 4 where the animals received 85 per cent. macerated dates and 15 per cent. sesame-seed-oil meal the rate of gain was less than satisfactory. Part of the reason may be the low crude-protein content of this concentrate mixture (see Table 8). In order to get a higher protein content it would be necessary to use less dates and more sesame-seed-oil meal. This should also improve the palatability and the dry-matter intake. Although the evidence from the second trial is based on a small number of animals, it is sufficient to encourage the investigation of the feeding value of higher proportions of macerated dates, to determine the maximum economical rate of substitution.

Ground date stones.—In the first trial the difference in the date-stone and non-date-stone feeds favoured the latter and although this difference is statistically significant at the 1 per cent. level (Tables 4 and 5), the comparison of the date-stone feed with all the non-date-stone feeds should be interpreted with caution. According to the limited information available in Table 1 the protein content of the date-stone feed would be somewhat less than the average of the other three feeds. In the higher-protein-soilage lots the difference in the gains produced by the feeds with and without date stones is much less pronounced (Table 4). In the second trial much higher levels of ground date stones (up to 85 per cent. in Lot 5) gave better results than some other mixtures containing

macerated dates (Table 7). In this case the protein content of the date-stone feed was higher.

There was a rather close agreement between the crude-protein percentages and the lot mean gains. Setting the crude-protein percentage at zero in Lot 6, the correlation coefficient between the protein percentages and lot mean gains is +0·96. The reduction in the sum of squares for lot means due to the regression of lot mean gains on protein percentages is 1081·1, a highly significant reduction. This leaves a remainder of 92·0 in the sum of squares for errors of estimate, with a mean square of 23·0 which is less than the mean square for individuals (Table 8). It thus appears that the differences in gain in this trial were closely associated with differences in protein content of the mixtures. Thus far, therefore, the evidence at least allows the conclusion that satisfactory rates of gain are possible when ground date stones form a substantial portion of the concentrate mixture.

Acknowledgements.—The authors wish to record the valuable contribution of the Date Association of Iraq which provided the dates and date stones for use in the feeding trials, and the machinery for mixing some of the feeds, as well as some of the labour. Particularly helpful in making the necessary arrangements to mix the date feeds were Mr. Frank Winter of the United Nations Food and Agriculture Organization Mission to Iraq and Dr. Ghazi Hamdi, Technical Director of the Date Association. Mr. Denha Iwass Mekhael, Director of the Agricultural Chemistry Section, Division of Soils, Abu-Ghraib Experiment Station, made the chemical analyses of the feeds used.

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A GLASSHOUSE SUITABLE FOR PHYSIOLOGICAL INVESTIGATIONS ON PLANTS GROWN IN THE TROPICS

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WITH PLATES 9 AND 10

Summary

The design and structure of a glasshouse suitable for physiological experiments under tropical climatic conditions are described. The glasshouse is partially open-sided, has a jack roof, and is supported by aluminium-alloy angle framework. All the metal parts employed, except for some iron-wire network, are of either aluminium or aluminium alloy. The glasshouse was easy to construct and requires the minimum of maintenance. The internal atmosphere of the glasshouse had lower maximum and higher minimum temperatures and a lower humidity than an adjacent area outside used for pot experiments.

The glasshouse proved to be satisfactory for experimentation with rubber seedlings, as indicated by their good growth and as judged by a study of the temperature and humidity of the internal atmosphere. Contamination of growing plants within the house by rust has been practically eliminated by the use of aluminium-alloy framework; consequently the glasshouse has proved most suitable for the production of micronutrient-element deficiency symptoms of rubber seedlings grown in sand culture. The design of the house has proved satisfactory and there has been no evidence, during its two years of use, of any excessive strain or defect in its constructional design.

THE objects of a glasshouse in temperate climates are to trap solar energy, and so conserve heat, and to advance the growth of the plants. Under tropical conditions the objective is different, the aim being to dissipate solar energy, not to accumulate it, and to attempt to reduce the internal glasshouse temperature to the same value as it is outside. Often the light available at certain seasons in temperate climates is below the optimal requirements of the plants but in Malaya, under tropical conditions, there is more than enough light available and some crops, for example tea and cacao, will grow better if the light intensity is reduced by various shading expedients.

The avoidance of high humidity is important, as in temperate climate glasshouses, but perhaps is not so critical because the atmospheric humidity in the tropics is usually high and any excessive or prolonged accumulation of water vapour is prevented by the high atmospheric temperature. In fact, in Trinidad, a humidifying apparatus is installed within the glasshouse and is used as a means of maintaining 100 per cent. humidity for the 'hardening' of young rooted cuttings of cacao [1]. A high humidity may have a slight effect in reducing insolation but an efficient rate of air movement through the glasshouse is probably of greater importance in the reduction of atmospheric temperature.

Experiments by Morris, Postlethwaite, Edwards, and Neale [2] have shown that there is a correlation between the total solar radiation received by various crops and the loss of water by evaporation, mainly by

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transpiration from the leaf surface. As the energy required for this evaporation is obtained from the sun it follows that a higher transpiration rate would promote a lower internal glasshouse temperature. If transpiration is enhanced by a more rapid air movement a more effective lowering of the air temperature by the plants should be obtained. Under temperate-climate conditions many growers may deliberately cut down the ventilation of their glasshouses, as increased ventilation would usually mean an increased heat loss and a danger of wilting [3]; however, under tropical conditions it would be expected that rapid air movement within the glasshouse might be a desirable and efficacious method of reducing the internal temperature.

The above general principles were used as guides in the design and construction of the glasshouse which is described below. Some information was available from other tropical countries, but this was insufficient upon which to base or copy a design; there was a lack of information regarding the performance of any such structures. The design of the glasshouse which was subsequently built was based originally on a drawing submitted by Mr. G. Owen, Head of the Soils Division; this drawing showed an open-sided, jack-roofed structure. This idea was later developed and expanded by the author in consultation with the architect, Mr. K. Smith-Mitchell, of Messrs. Palmer and Turner, Architects, Singapore. There was little available information as to whether rubber plants could be grown under glass in full tropical sunlight and it was not certain whether they could be grown successfully in sand culture under those conditions.

The construction of the glasshouse was completed in 1954 and it has been in service since December of that year. It was intended for the study of the growth of rubber seedlings in sand culture under micronutrient-element deficiency conditions; for this purpose it has proved very satisfactory. It has been possible to grow healthy rubber plants in the glasshouse up to the age of 12–15 months without any difficulty due to detrimental environmental factors, such as overheating.

Design and Construction of Glasshouse

It was decided to orient the glasshouse in a north–south direction. This decision was partially a matter of convenient siting, as it was not expected that orientation would be an important factor in a latitude of 3° N., and partially because the arguments which favour the east–west orientation of temperate-climate glasshouses did not operate here. Thus our concern was not to collect light during winter months but rather to ensure that all light received was evenly distributed within the glasshouse. Early morning and late afternoon sunlight would be expected to operate for short periods of time but this would affect the whole of the long sides of a north–south house but only the two ends of an east–west house. Photographs of the glasshouse, as finally sited, are shown in Figs. 2 (*a*) and 2 (*b*) (Pl. 9).

The glasshouse was built 60 ft. long and 30 ft. across (Fig. 4); it has a minimum height, above ground level, of 10 ft. but in the middle section of the glasshouse the head space is much greater. The roof is equipped

with one jack roof which is set at an angle different from that of the main roof (Fig. 5). The upper two-thirds of each of the long sides of the glasshouse are covered with iron-wire network but are otherwise open; the lower third, with the exception of a 3-in. clearance at the bottom, is covered by corroplast sheeting (a compressed fibre material). Thus a large proportion of the long side walls is open and allows for abundant air movement into the glasshouse. On the other hand, due to the considerable overhang of the eaves, very little rain can drive into the glasshouse. The short sides, or transverse ends, of the glasshouse would not (because of the proportionately smaller overhang of the roof in relation to the area of side exposed) be so well protected from rain if the same

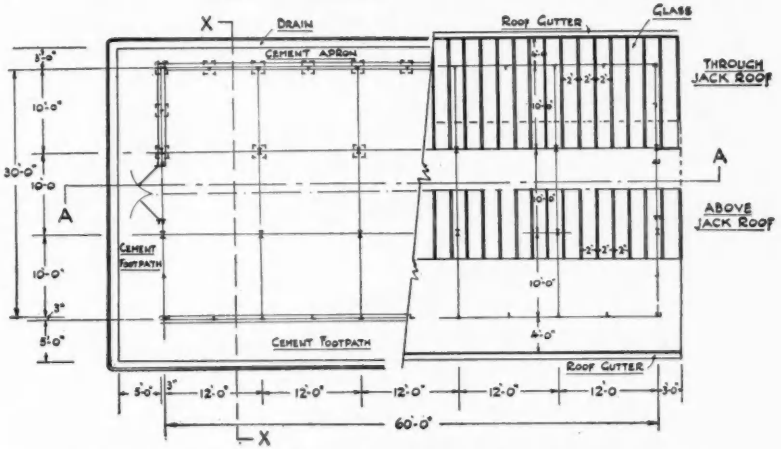


FIG. 4. Partial roof and floor plans of glasshouse, benches not shown.

proportion of open space was maintained. Consequently glass 'naco' louvres were installed, in place of most of the iron-wire network, in the end walls of the glasshouse; these louvres can be shut as desired in times of heavy rain, and are disposed as indicated in Fig. 5.

As the glasshouse was intended for micronutrient-element deficiency experiments it was desirable to use aluminium rather than iron or steel for the structural framework. It would also have been preferable to use aluminium-wire gauze rather than the iron-wire network for the protection of the open sides but as the former could not be obtained locally the iron-wire network (approximate mesh size: 3 in. × 1 in.) dipped in bitumen, was used in its place. With the exception of this iron-wire network, all the metal framework used is constructed of aluminium-alloy angles ($3\frac{1}{8}$ in. × $1\frac{5}{8}$ in. × $\frac{3}{32}$ in.), see Fig. 1 (Pl. 10). The glazing bars, the bars used to hold the glass panes in position, the guttering, and the ridgepiece are also made of aluminium. The nuts and bolts used are made of aluminium alloy. Thus almost all the metal used in the construction is non-ferrous; it is unlikely that these rust-proof materials will contaminate any growing plants and hence vitiate the validity of an experiment.

The alloy is of light weight and accordingly the structural strength of the glasshouse, to a large extent, depends on the pattern in which the alloy angles are united. Figs. 6 and 7 represent a cross- and longitudinal-section, respectively, of the glasshouse; they illustrate the assembly of the component parts. The ease of assembly, by comparatively unskilled labour, and the light weight of the alloy angles confer big advantages as compared with the use of steel; much less weight and bulk of material were required and, owing to the ease of packing the angles, the cost of transport of the materials was much reduced.

Clear glass (30 oz./sq. ft.) was used as roofing material; this glass did

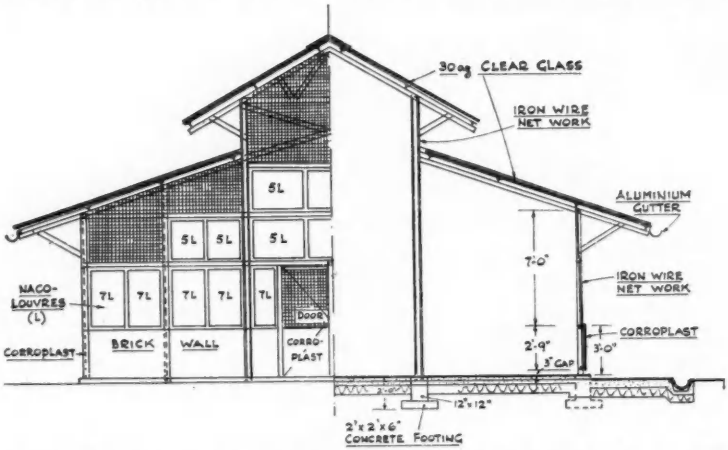


FIG. 5. Half elevation of gable end combined with half cross-section of glasshouse.

not possess any exceptional properties except that it was relatively cheap and could be purchased locally. The glasshouse roof panes measure 5 ft. 7 in. by 2 ft.

The floor of the glasshouse slopes gently away from the north–south centre line of the glasshouse; this slope, at an angle of approximately 20 minutes, prevents the accumulation of water. Nine benches, each 12 ft. × 3 ft. × 1½ ft., are arranged alternately on either side of the gangway in the southern half of the glasshouse; in the northern half, four benches, each 11 ft. × 3 ft. × 1½ ft., were erected to run longitudinally, two on either side of the gangway. The benches are composed of brick, rendered with plaster and, where necessary, were built around the uprights, thus adding to the rigidity of the structure.

The above account is not intended to be an exhaustive description of the design of the glasshouse; further details may be obtained from the architects. It is estimated that the cost of the whole glasshouse including site preparation, footpaths, concrete aprons, flooring, benches, angle framework, architect's fees, and labour amounted to 27,000 Malayan dollars (approximately £3,000 sterling). The glasshouse design, described above, presented a practical and economical solution to our

special requirements; it also requires a minimum of maintenance, such as painting. It is estimated that a saving of approximately 10,000 Malayan dollars (£1,200 sterling) has been made as compared with a similar building supported by steel or reinforced concrete.

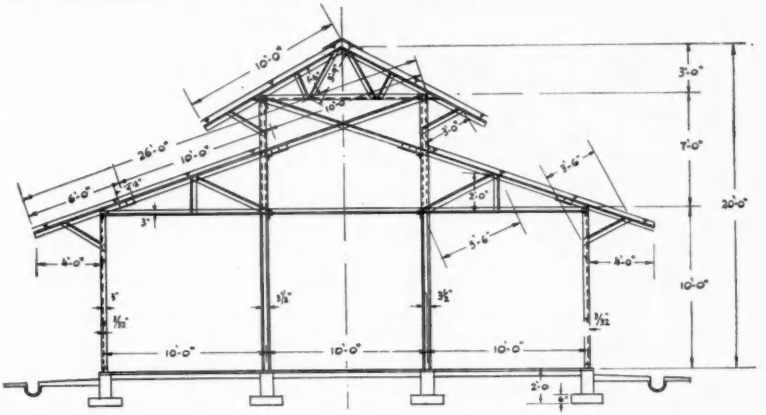


FIG. 6. Cross-section taken across glasshouse (along line X–X, Fig. 4).

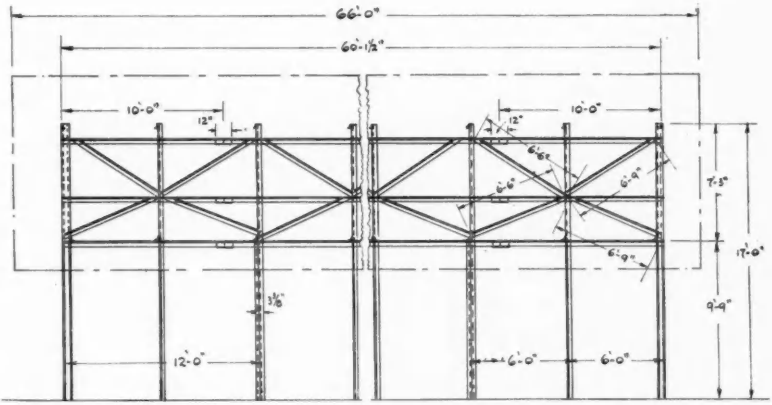


FIG. 7. Part of longitudinal-section taken through glasshouse (along line A–A, Fig. 4).

The Efficiency of the Glasshouse

The main and most practical criterion of efficiency is whether plants grown inside the glasshouse are as healthy and as free from disease as those grown outside. It was found that plants supplied with 'complete' nutrient and grown within the glasshouse were, in fact, the healthiest and largest so far raised by us in sand culture under Malayan conditions. In one particular experiment, unselected but 'selfed' Tjir. 1 seedlings

supplied with a 'complete' nutrient solution and grown in 3½-gallon containers possessed an average girth (7 cm. above sand level) of 8·2 cm. 12 months after the seed was sown. Hand-pollinated seedlings 13 months old, from good parents, grown in the field at our Experiment Station, were found to possess a corresponding girth of 9·9 cm. The glasshouse-grown plants were thus smaller than those grown in the field, where there was no limiting factor of pot size on root development. Thus the comparison was not a strict one, but it did serve to indicate that glasshouse-grown plants were not seriously inferior to field-grown plants. Fig. 3 (Pl. 10) shows typical plants grown in the glasshouse.

Outstanding success was also achieved in the production of copper- and zinc-deficient rubber plants. It seems doubtful whether the same success could have been achieved if the plants had been freely exposed to atmospheric contamination and not grown within the glasshouse.

Apart from these visual assessments of the efficiency of the glasshouse some measurements of temperature, humidity, and light were also made.

Temperature.—Temperature measurements were made with two standard-pattern thermographs. One was placed in the centre of the glasshouse and the other in the centre of an open pot enclosure in line with the glasshouse but 113 ft. to the south. Both thermographs were screened so as not to receive direct sunlight and both were placed at a height of approximately 3 ft. above ground-level. Rubber plants, grown in sand culture, were situated on benches within the pot enclosure; the conditions were representative of those formerly used for plant-nutrition experiments before the glasshouse became available. Both thermographs were situated near to growing plants; the essential difference was that one was in the glasshouse and the other placed outside, but otherwise under closely similar conditions.

For each month of 1955 records of glasshouse and pot-enclosure temperatures are shown (Fig. 8). These temperatures are average values based, usually, on the number of complete weeks within each month; the number of weeks over which data are averaged is indicated for each month. The data, which are nearly complete with the exception of the earlier months, show the extent of the daily and monthly variation. One markedly consistent feature was that the temperature of the pot enclosure fell to a lower value at night than that of the glasshouse. This difference, which attained a maximum of 4–5° F., was sometimes detectable at 08·00 hours. On the other hand, the pot enclosure maximum was usually higher than that of the glasshouse. This was particularly so for the earlier, hotter, part of the year but for November and December it was sometimes noted that the glasshouse maximum temperature was slightly higher than the enclosure value. This was attributed to the very heavy rainfall during these two months, a factor which tended to depress the external temperature more than the glasshouse temperature. For the very warm months of February and March the maximum daily temperature recorded in the pot enclosure was sometimes as much as 8–10° F. higher than the corresponding maximum recorded for the glasshouse.

No attempt will be made to analyse further the daily temperature variation, as the wealth of accumulated data, summarized in Fig. 8,

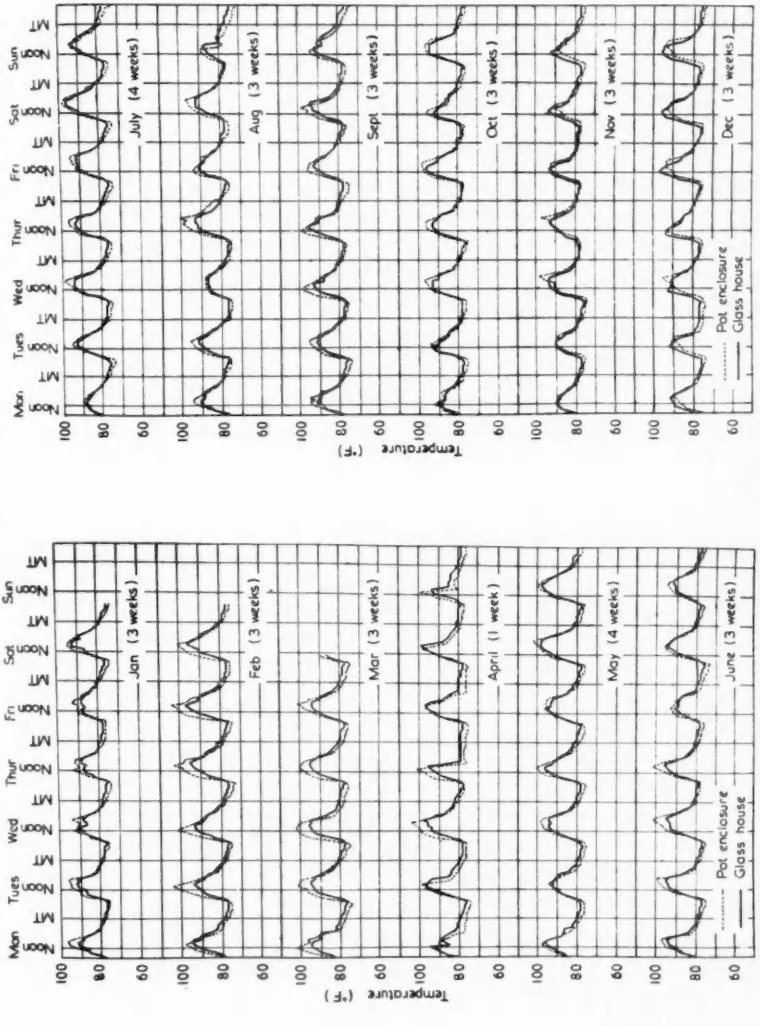


FIG. 8. Summary of daily temperature variations recorded for glasshouse and pot enclosure during 1955. The values are means of readings taken over the number of complete weeks for which records were available; this number is indicated for each month.

clearly answers the purpose of this investigation. It was clear that, generally, the glasshouse temperature did not exceed that of the pot enclosure, except at night, and the maximum daily temperatures were higher outside than in the glasshouse.

Humidity.—The humidity measurements were obtained with a whirling hygrometer and were taken on three occasions during the day. Measurements were made in each quarter of the glasshouse and pot enclosure and adjacent to each respective thermograph. The pot enclosure measured 60 ft. × 50 ft.; the approximate distances apart in the north–

TABLE 1. *Relative Humidity Values taken in 1956. Each Value Represents Mean of Values taken in five different positions*

Time	*Glasshouse*			*Pot enclosure*		
	08.30	12.00	15.30	08.45	12.15	15.45
Feb. 17	87	59	51	91	60	53
,, 20	77	54	75	87	58	98
,, 21	86	57	68	86	61	68
,, 22	88	63	69	89	68	Rain
,, 23	85	64	48	88	65	51
,, 24	82	53	54	85	55	50
,, 27	87	55	49	87	53	50
,, 28	79	50	44	84	52	44
,, 29	72	49	45	66	48	45
Mar. 1	74	44	39	78	43	39
,, 2	79	49	43	82	55	48
,, 5	81	49	62	87	53	64
,, 6	40	53	48	43	56	50
,, 7	87	57	46	89	60	50
,, 8	89	62	60	96	65	68
,, 9	82	56	47	87	57	49
,, 12	78	57	54	79	60	59
,, 13	74	56	53	81	57	54
,, 14	86	56	47	90	62	55

south direction between the points at which humidity readings were taken were roughly similar to those for the glasshouse, but the distances apart in the east–west direction were greater for the enclosure than for the glasshouse. A summarized version of some of the values obtained in 1956, when quite tall plants were growing in the glasshouse, is presented in Table 1.

Early-morning humidity was higher in the pot enclosure than in the glasshouse; this difference could persist into the afternoon. It is probable that the warmth retained by the glasshouse overnight prevented the atmosphere achieving the humidity of the external air in the early morning.

In general, the records showed that the glasshouse humidity was slightly less than that of the pot enclosure.

Light.—Instruments to measure the exact light intensity within the glasshouse were not available but an approximate estimation was obtained with the aid of a Weston Master II Universal Exposure Meter. Light

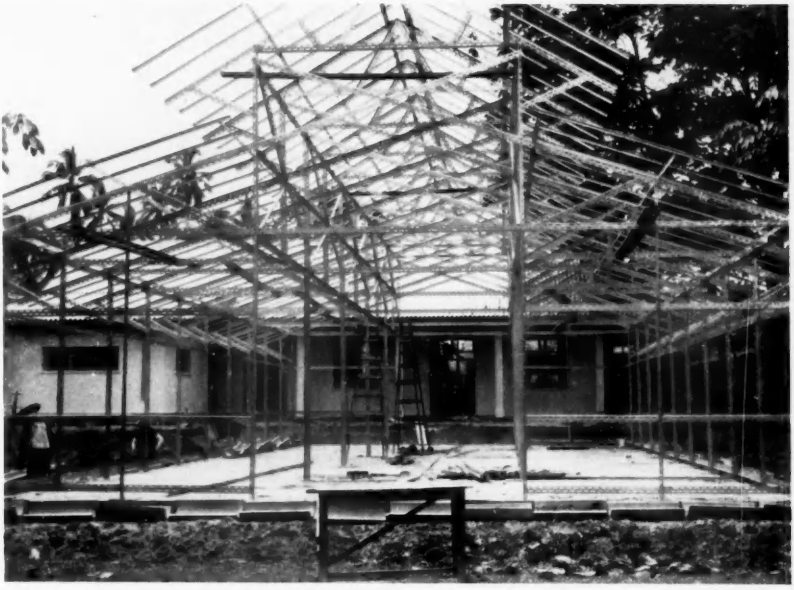
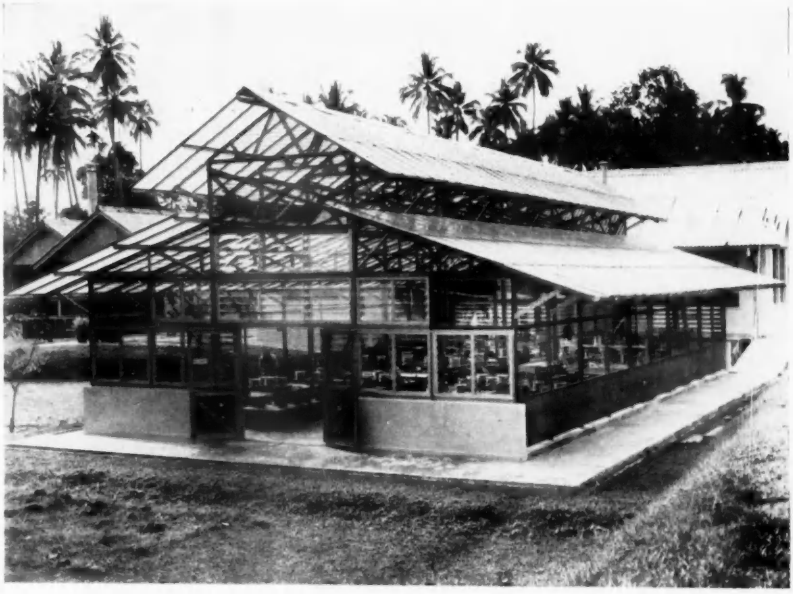
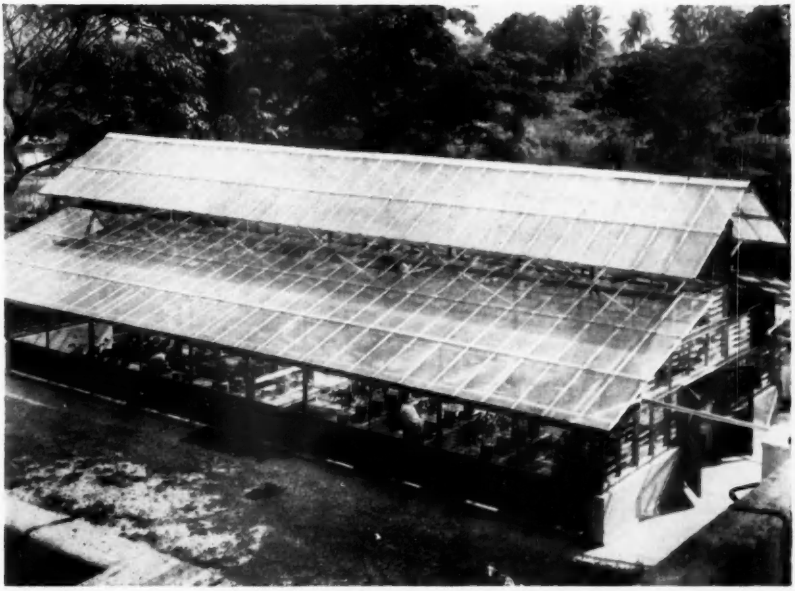


FIG. 1. Glasshouse in early stage of erection. Note use of aluminium alloy angle framework.

FIG. 3. Photograph taken within the glasshouse, facing south. Young experimental plants in foreground, older ones in background.



(*a*)



(*b*)

FIG. 2. Completed glasshouse. (*a*) Oblique end view. (*b*) Oblique side view, from above. Note long overhang of eaves, glass louvres in end or transverse sides, and iron wire network along open portion of sides of glasshouse.

values were recorded for the early part of 1956 and were taken at the same times and in the same positions, in the glasshouse and pot enclosure, as used for the humidity determinations.

It was found that during the early morning (08·30 hours) and afternoon (15·30 hours) the light intensity within the glasshouse was approximately one-half of that recorded for the pot enclosure. However, towards midday (12·00–12.30 hours), when the sun was almost directly overhead, the glasshouse values were only slightly less than the values obtained in the pot enclosure.

The midday light intensity in the pot enclosure was approximately 5–8 times greater than that of the early morning but for the glasshouse the corresponding values were 8–12 times. These results showed that the morning sun was relatively less effective in penetrating into the glasshouse than at midday.

The diminution in light intensity noted for the glasshouse during morning and afternoon was not a critical disadvantage; it did not impede plant growth nor did it render the plants more susceptible to disease but it did mean that, to some extent, the plants were grown under light shade. This reduction in light intensity was due to the discoloration of the glass mainly caused by accumulated layers of dirt, which had taken place in the course of two years after glazing.

Acknowledgements.—I thank the Director, Deputy Director, and the Head of the Soils Division of the Rubber Research Institute of Malaya for their encouragement and every administrative help during the period in which the glasshouse was planned and built. Figs. 4, 5, 6, and 7 are based on working drawings supplied by the Architects, Messrs. Palmer and Turner of Singapore.

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